THE INFLUENCE OF ENVIRONMENTAL FACTORS ON THE REPRODUCTIVE OUTPUT OF PEREGRINE FALCONS IN THE YUKON

Brett A. Boukall
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APPROVAL

Name: Brett Boukall

Degree: Master of Science

Thesis Title: THE INFLUENCE OF ENVIRONMENTAL FACTORS ON THE REPRODUCTIVE OUTPUT OF PEREGRINE FALCONS IN THE YUKON

Exhmining Committee:

Chair: Dr. Robert Tait
Dean of Graduate Studies
University of Northern British Columbia

Supervisor: Dr. Russell Dawson, Associate Professor
Natural Resources and Environmental Studies Program
Canada Research Chair, Avian Ecology
University of Northern British Columbia

Committee Member: Dr. Katherine Parker, Associate Professor
Natural Resources and Environmental Studies Program
Ian McTaggart Cowan Muskwa-Kechika Research Professor
University of Northern British Columbia

Committee Member: Dr. Michael Gillingham, Associate Professor
Natural Resources and Environmental Studies Program
University of Northern British Columbia

Committee Member: Dave Mossop, MSc, Biology Instructor
Arts and Science Division
Yukon College

External Examiner: Dr. Karen Wiebe
Associate Professor, Department of Biology
University of Saskatchewan

Date Approved: May 5, 2006
ABSTRACT
Recent variation in the reproductive output of Peregrine Falcons (*Falco peregrinus anatum*) breeding along the Yukon River has encouraged the examination of the environmental factors that influence the reproductive ecology of these birds. The objectives of this study were to examine how weather, territorial quality and prey selection by breeding Peregrine Falcons relate to productivity at nest sites. I also assessed territorial occupation frequency as a measure of habitat quality. A total of 52 territories were monitored along the Yukon River, and were surveyed 11 times from 1984-2004. The occupation frequency was highly correlated with measures of productivity at a nest and I therefore considered occupation frequency to be a good measure of territorial quality. The annual average quality of occupied territories explained 53.6% of the variation exhibited in the mean annual number of fledged young and provides support for the theory of site-dependent regulation. Precipitation during the late nestling stage, and a forest fire that occurred in 2004, however, were also very important in determining the mean annual reproductive output. This study also provided evidence that breeding Peregrine Falcons are selective predators. Pairs brought more biomass to nests on territories that produced a greater number of young, and exhibited less diversity in their diet, implying that selected prey was more accessible, parental foraging was selective and efficient, or possibly a combination of both. Given the number of high-quality sites available and the peregrine’s ability to selectively forage, there is a positive outlook for Peregrine Falcon populations in the Yukon.
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1. GENERAL INTRODUCTION

DETERMINANTS OF POPULATION DYNAMICS: MECHANISMS OF DENSITY-DEPENDENT AND INDEPENDENT PROCESSES

To fully understand what mechanisms regulate and limit population growth, it is necessary to determine how variable environmental conditions influence population dynamics. The majority of studies have focused on the distribution and abundance of resources (i.e., food and habitat) in the environment and the regulation of population size through density-dependent resource competition (Krebs et al. 2001). The underlying mechanisms of regulation, however, are not well understood even in well-studied organisms (Murdoch 1994), such as the Peregrine Falcon (*Falco peregrinus*).

Interference competition, where density inversely relates to population growth (Lack 1966), has been widely suggested as a means for population regulation. This density-dependent hypothesis suggests that increased density results in increased intra-specific competition for resources, though the actual mechanism of regulation (crowding, territoriality) is not always clear (Rodenhouse et al. 1997). Recently, new ideas have addressed the influence of resource quality and abundance as a mechanism of density dependence in populations (Rodenhouse et al. 1997). This hypothesis typically involves central-place foragers, and as such has centered on populations of birds. This hypothesis focuses on the differing quality of resources available for use by breeding members of a population and predicts that as density increases, new individuals use lower quality resources more frequently. The increased use of lower quality resources can result in increased variation in the average productivity of the population (Newton 1998). Other
factors exist, however, that can affect population growth regardless of the breeding density. These density-independent factors, such as adverse weather conditions, influence the survival and fitness of individuals exposed to these conditions (Sutherland 1996). The combined influences of both density-dependent and density-independent factors act simultaneously to influence population growth. To fully understand the causes of variation in size of a population, it is necessary to comprehend how these processes interact to influence population dynamics.

HABITAT HETEROGENEITY AND TERRITORIAL QUALITY

A major obstacle in examining density-dependent interactions in bird populations has been defining and measuring habitat or territorial quality. Territorial quality refers to the environmental characteristics of a region or territory that influence the fitness of organisms occupying the habitats within a territory (Pulliam 1988). Features such as resource availability, protection from predators and protection from environmental conditions all contribute to the quality of habitat and, subsequently, the fitness of individuals. Higher quality habitat can be ascribed to those territories that offer greater abundance of resources, resulting in higher fecundity and survival. Due to the nature and limited availability of high-quality territories, one can predict high-quality territories should be occupied more frequently than lower quality territories (Rodenhouse et al. 1997). In addition, individuals that successfully breed at a site are more likely to return in a future breeding season (Hass 1998). Therefore, the occupation frequency of a territory may provide an index of territorial quality (Sergio and Newton 2003).
Ecosystems tend to be heterogeneous at varying scales (Sutherland 1996) and this heterogeneity leads to variation in resources of the habitat sites occupied by different individuals. Habitat heterogeneity and patterns of occupation have also been used to explain density dependence in populations (see review in Newton 1998). The competition for finite resources among individuals leads to territories of differing quality being occupied, thus influencing the survival and productivity of individuals. Increased population size will result in increased use of poorer habitat, leading to a reduction in overall productivity, or mean number of fledged young (Both 1998). The decrease in average population productivity due to the differences in territorial habitat quality has been termed ‘site-dependent regulation’ (Rodenhouse et al. 1997).

DENSITY-INDEPENDENT INFLUENCES ON PRODUCTIVITY

There are factors in the environment that are unrelated to the density of individuals that can also influence productivity of bird populations. These density-independent factors, such as weather, can play an important role in the fluctuations of a population (Sutherland 1996). Variation in weather can affect breeding rates in birds mainly by influencing the parents’ ability to forage or by affecting activity levels of prey (Nilsson 1982, Elkins 1983, Murphy 1987, Mearns and Newton 1988). In addition, inclement weather increases the energy requirements for thermoregulation of the young, increasing the need for food (Royama 1966). Extreme weather events during the breeding season, which are common in more northerly latitudes, may also result in the direct mortality of individuals and young in a population (Ojanen 1978, Court et al. 1988, Bradley et al. 1997).
RELATIONSHIP BETWEEN FOOD RESOURCES AND TERRITORIAL PRODUCTIVITY

Food availability often determines the reproductive output of organisms, and thus has a great potential to regulate density of populations (Sutherland 1996), including those of birds (Hogstedt 1981, Martin 1987, Korpimäki 1989). Many studies have focused on the relationship between food supply and productivity in raptor species (Newton and Marquiss 1981, Dijkstra et al. 1982, Korpimäki 1989, Dawson and Bortolotti 2000). Raptors are good subjects to examine responses to food supply because they are often easy to observe, they leave prey remains and pellets, which allow for identification of prey items, and as top predators they may be more sensitive to environmental perturbations (e.g., DDT and habitat change) (Newton 1979).

The degree to which raptor populations fluctuate is often determined by their responses to changes in prey density (see review in Newton 1979). Species such as rodent-eating raptors, for which the food supply fluctuates dramatically, can exhibit large annual variations in breeding success (Newton 1979). Specialist predators such as Gyrfalcons (*Falco rusticolus*) have narrow dietary niche widths. As the density of their selected prey, Willow Ptarmigan (*Lagopus lagopus*), fluctuates, so does their annual production of young, varying three-fold from year to year (Newton 1979). Conversely, generalist species such as Peregrine Falcons have greater dietary niche widths and can respond functionally to changing prey density by switching prey species and consumption rates. Species such as Peregrine Falcons should show less reproductive variation in response to fluctuations in prey compared to predator species that respond numerically (Mindell et al. 1987).
Optimal foraging theory (MacArthur and Pianka 1966, Krebs 1978) would predict that generalist predators should select for prey types in the landscape that are energetically profitable and abundant (Morse 1990). If prey items are variable in abundance and availability, predators should switch to the next most profitable prey type when the density of their selected prey decreases (Murdoch and Oaten 1975, Korpimäki et al. 1991). This broadening of the diet reduces the dependence on any one prey species, thus mitigating the influence of prey fluctuations on the productivity of a population (Stephens and Krebs 1986).

It may be misleading to define a species as a generalist predator because many of the prey items used may share similar habitat associations, distributions and size characteristics (Mindell et al. 1987). Additionally, dietary niche width may not necessarily be indicative of selected prey abundance and may not ensure population stability when many of the selected prey items fluctuate simultaneously (Mindell et al. 1987). Wider dietary diversity may indicate lower abundances of selected prey types, therefore forcing predators to forage for alternative and less advantageous prey types (Stephens and Krebs 1986).

The heterogeneity of the landscape results in spatial variation of food resources available to breeding individuals, which in turn can affect the production of young (see review in Newton 1998, Krebs et al. 2001). Therefore, the variation in productivity exhibited among territories in a population may be the result of different prey availabilities on individual territories (Rodenhouse and Holmes 1992, Dawson and Bortolotti 2000). Few studies, however, have examined the relationship between
productivity and the food supply available on the territory in explaining reproductive variation among individuals in a population.

POPULATION LIMITATION AND REGULATION IN BIRDS

Since density-dependent processes were first theorized by Lack (1954, 1966) and Ashmole (1963), studies examining population regulation have frequently investigated the dynamics of bird populations (Newton 1998). The majority of research to date has examined non-migratory species, despite the fact that migratory species comprise the majority of birds inhabiting temperate areas (Sherry and Holmes 1995). Recent studies (Rodenhouse et al. 2003, Sergio and Newton 2003) have examined regulation in populations of migratory species, and stress the need for long-term demographic data that can be used to examine the mechanisms and process of population regulation (Rodenhouse et al. 2003). Density-dependent regulation has been observed in many territorial bird species, and in many studies on raptor population dynamics (Newton and Marquiss 1986, Newton and Marquiss 1991, Ferrer and Donazar 1996, Fernandez et al. 1998, Krüger and Lindström 2001).

Understanding the mechanisms that determine population fluctuations is an important concept in both ecology and conservation biology. Given that prey abundance, territorial quality, weather and nest-site characteristics are not mutually exclusive and can vary together, it is important to determine how these factors interrelate to influence the breeding dynamics of populations. The aim of this thesis was to examine how natural processes interact to regulate and limit the productivity of Peregrine Falcons (F. p. anatum). This species is a generalist predator that often breeds along river valleys,
making it highly visible. Additionally, long-term data sets on population dynamics are available for many areas, allowing territorial occupation to be examined. Populations of Peregrine Falcons, therefore, serve as an excellent model to examine the influences of prey selection, territorial quality and weather on reproductive output.

I studied a remote population of Peregrine Falcons breeding along the Yukon River, Yukon Territory, and also used a long-term data set documenting the dynamics of the population (D. Mossop, unpubl. data). My primary objective in this study was to determine how prey abundance, habitat quality and weather influence the reproductive output of Peregrine Falcons, and how these factors interrelate. A secondary objective was to examine whether the use of occupation frequency was a good measure of habitat quality (Sergio and Newton 2003) and to identify territories of high quality for future conservation purposes.

STUDY SPECIES
PEREGRINE FALCONS

The Peregrine Falcon is a medium-sized bird of prey, having one of the largest distributions of all avian species. Peregrines breed on every continent except Antarctica, and on most major island chains with the exception of New Zealand and Iceland (Ratcliffe 1993). The global distribution of the Peregrine Falcon is due, in part, to its correspondingly broad diet of predominantly avian species (Newton 1979, Ratcliffe 1993).

Despite being described as a generalist and opportunistic feeder (Newton 1979), the Peregrine Falcon is a morphologically and behaviourally specialized predator of open
environments (Cade 1982, Jenkins 1998). Peregrine Falcons hunt from elevated perches or high-soaring positions and use their heavy bodies and streamlined shape to descend in rapid dives to strike and capture prey in mid-air (Ratcliffe 1993). Therefore, natural populations of Peregrine Falcons are largely distributed in open environments, often near coastal and riverine cliffs.

Remnants of prey brought to feed the nestlings usually remain on or near the nest ledge. These provide the researcher with an opportunity to observe the use of prey by breeding Peregrine Falcons during the nestling period. Additionally, the identification of perches used to pluck prey can provide more information on the diet of breeding Peregrine Falcons.

POPULATION DYNAMICS IN THE YUKON

Peregrine Falcons typically arrive on their breeding grounds in the Yukon in early May, and courtship begins soon after arrival (Cade 1960). Clutch initiation usually occurs by mid-May in most territories. In temperate latitudes, incubation usually begins after laying the penultimate egg (Ratcliffe 1993), but at higher latitudes incubation may begin after the first or second egg is laid, depending on conditions (Court et al. 1988). Incubation lasts approximately 33 days (Cade et al. 1996). The female falcon performs most of the incubating duties, although the male may incubate for several hours per day. General accounts of breeding behaviour in Peregrine Falcons indicate that females perform the majority of brood-rearing duties, while males conduct most of the hunting (Nelson 1977, Palmer 1988, Ratcliffe 1993). Prey items are usually transferred in mid-air and the female will feed away from the nest ledge (Nelson 1977).
The average hatching date for this study population along the Yukon River was June 13 (B. Boukall, unpubl. data). The young are unable to thermoregulate effectively until they reach approximately 21 days of age (Enderson et al. 1972). After this period, the female will assist the male in foraging and generally is able to capture larger prey items, which may be related to sexual size dimorphism in this species. Females (~900 g) weigh almost one third more than males (~600 g) (Ratcliffe 1993). Fledging generally takes place after 42 days (approximately mid to late July), although female young may take slightly longer due to their larger size and slower development (Nelson 1977).

There has been a great deal of interest in the reproductive performance of various populations of Peregrine Falcons in the past four decades (Hickey 1969, Cade and Fyfe 1970, Court et al. 1988, Ratcliffe 1993). Most of the variation in productivity has been linked to contamination by pesticides, of which Peregrine Falcons are particularly sensitive (Newton 1979, Ratcliffe 1993). From the late 1940’s to early 1970’s, massive use of organochlorine pesticides, particularly DDT in agriculture and forestry, resulted in bioaccumulation of toxic residues in prey species. These residues in turn concentrated in falcons, causing both lethal and sub-lethal effects (see reviews in Cade et al. 1988). In arctic Canada from 1981 to 1985, eggs from failed nests had shells averaging 20.2% thinner than normal, while eggs from successful nests averaged 16.1% thinner (Court et al. 1990). Subsequent recovery of populations of Peregrine Falcons in the late 1980’s was associated with reduced pesticide residues in the prey, eggs and body tissues of falcons, resulting in increased eggshell thickness, and increased productivity (Cade et al. 1988, Court et al. 1990, Peakall et al. 1990, Mesta 1999). The recovery of Peregrine Falcons in almost all regions of their range has allowed greater attention to be focused on other
factors influencing their reproductive success. The effects of factors such as weather, nest-site habitat characteristics, prey density and the selection of prey on the reproductive output of peregrines have received relatively little attention (Newton 1988, Olsen and Olsen 1989a, Ratcliffe 1993, Redpath and Thirgood 2000). Recent variations in the reproductive success of the *anatum* subspecies of Peregrine Falcon in the northern portions of its range has encouraged the examination of environmental factors and their effects on reproductive success in more detail (Mossop 2001).

The rapid re-colonization of the Yukon River valley by peregrines has resulted in present numbers of breeding birds exceeding the pre-crash population (Mossop 2001). This appears to be a common trend among recovered populations of peregrines, with many populations surpassing their historical levels (Ratcliffe 1993, Kirk and Hyslop 1998). From 2000-2002, productivity in the population of peregrines along the Yukon River varied, with 35 to 73% of the occupied territories producing young. The cause of this dramatic variation remains unknown, and may be a result of environmental fluctuations. A large amount of variation in the use of prey by individual breeding Peregrine Falcon pairs was observed (B. Boukall, unpubl. data) and provides a possible explanation for the variation in productivity. Many studies have examined food habits of peregrines, but there has been little research to suggest that individual prey selection can influence the productivity of Peregrine Falcons.

THESIS OUTLINE

My study attempted to determine the causes of variation present in the productivity of Peregrine Falcons breeding along the Yukon River, and focused on the influence of
weather, habitat, and prey selection. In particular, this thesis determined how these factors interrelate to determine the reproductive success of peregrines. Several studies have examined the role of each of these factors in determining reproductive output of peregrines (Olsen and Olsen 1989a, b), but no studies have been conducted in the Yukon.

Density-dependent limitation of habitat has been widely suggested as a means for population regulation. The exact mechanism of regulation, however, is poorly understood, although site-dependent regulation (Rodenhouse et al. 1997), whereby the quality of habitat available to potential breeders limits the overall population productivity, may be important. Nonetheless, the productivity of many bird species can be influenced by weather conditions, which can affect populations independent of density. In Chapter 2, I examine variation in reproductive output of Peregrine Falcons, and apply the site-dependent regulation model (Rodenhouse et al. 1997) as a possible explanation for the variation observed. In addition, I also examine the effects of weather and nest-site characteristics in determining productivity of the population. I use a long-term data set on occupation frequency of territories in my population as a measure of habitat quality (Sergio and Newton 2003).

Most studies have indicated that peregrines appear to use prey resources disproportionately to their availability (Johnson 1980, Hunter et al. 1988, Rosenfield et al. 1995). Prey selection by peregrines can vary among populations, habitats and even individuals (Ratcliffe 1993), and variable reproductive output may be due to the selection of prey by territorial peregrines. Those pairs selecting prey that is either low in abundance or not energetically beneficial should perform poorer than those selecting for energy-efficient prey that is relatively abundant. In Chapter 3, I investigate the selective
feeding of peregrines relative to the abundance of prey groups on individual territories. I examine prey use, dietary niche breadth, and territorial prey abundance and relate these components to reproductive output.

The interaction and synthesis of the effects of habitat, food preference and availability, and weather are discussed in Chapter 4. I explore how these factors act simultaneously to influence the dynamics of populations of Peregrine Falcons in the northern boreal forest. The preferential use of habitat and prey may result in differences in productivity between pairs, thus having evolutionary consequences. The conclusions reached by this study are directly applicable to the changing climatic conditions of the north, and conservation management issues of ecological and population integrity are also discussed.
INTRODUCTION

Stability of animal populations over time is usually attributed to factors that regulate and limit further growth of the population (Lack 1954). Competition for finite resources in the environment, such as high-quality habitat, can regulate the growth of a population by influencing the reproductive output of individuals. The ideal despotic model of distribution (Fretwell and Lucas 1970) theorizes that high-quality individuals in good condition should be the first to occupy the best-quality sites, relegating individuals in poorer condition to habitats of lesser quality. This process implies local source-sink dynamics in that a threshold exists in the amount of high-quality habitat available to a population (Pulliam and Danielson 1991). Individuals occupying poorer quality habitat tend to be exposed to higher rates of mortality, and are less likely to produce offspring (see review in Newton 1998). As population growth continues, new individuals are continually relegated to habitats of lesser quality. Some individuals may forego breeding because the cost of maintaining a poor-quality territory exceeds the possible benefits of breeding in such habitat (e.g., Haas 1998). Those that do breed in low-quality territories, however, frequently experience lower nest success (Bollinger and Gavin 1989, Haas 1998), which results in an overall decline in the average productivity of the population, thus regulating population size and growth (Rodenhouse et al. 1997).

The combination of habitat heterogeneity, ideal despotic distribution of individuals and density-dependent productivity has been termed ‘site-dependent population regulation’ (Rodenhouse et al. 1997), whereby the mechanism of regulation in
a population is limited high-quality sites available for breeding. The majority of studies evaluating this hypothesis have focused on populations of birds, particularly raptor species. This hypothesis predicts that productivity in high-quality sites is independent of population density surrounding the site. As density increases, however, the increased usage of low-quality breeding territories results in a decline in mean productivity of the population (Sergio and Newton 2003).

One of the key features necessary to test the site-dependent regulation hypothesis (Rodenhouse et al. 1997) is the identification and measurement of habitat quality inhabited by a breeding pair of birds (Sergio and Newton 2003). Habitat quality can be used to refer to the environmental characteristics of a region or territory that influence the fitness of individuals occupying that habitat (Pulliam 1988). Features such as resource availability, protection from predators, and protection from environmental conditions all contribute to the quality of habitat and subsequently the fitness of individuals. The density of individuals occupying a habitat has been commonly used as an indicator of habitat quality, but population density alone may not accurately reflect the influence of habitat quality on fitness and fecundity of individuals (Van Horne 1983). For example, subdominant individuals may be forced into lower quality habitats, and so densities may actually be higher in these low-quality environments (Van Horne 1983). Alternatively, in territorial species, the usage frequency of a particular territory by organisms may reflect the value of the inherent characteristics and resources of the habitat to individuals occupying a particular region (Sergio and Newton 2003). Those territories that offer a greater abundance of resources, resulting in increased survivorship and fecundity, will be used more frequently than other territories (Pulliam and Danielson 1991). Hence, the
quality of the habitat in a particular territory may be estimated on the basis of occupation frequency and should be related to reproductive output of individuals breeding in a particular territory (Sergio and Newton 2003).

Territorial quality alone, however, may not effectively explain the fluctuations exhibited by populations, due to influences of density-independent processes. Density-independent processes, such as weather conditions during the breeding season, can affect the dynamics and breeding rates of a population (Sutherland 1996, see review in Newton 1998). As a result, current population densities may simply mirror recent short-term variation in environmental conditions, instead of limitations of quality habitat (Van Horne 1983). In raptors, for example, variation in climatic conditions during the breeding season can influence the productivity of a population by affecting the foraging ability of adults and survival of nestlings (Stinson 1980, Murphy 1987, Mearns and Newton 1988, Steenhof et al. 1997, Dawson and Bortolotti 2000). Favourable weather conditions during the breeding season may mitigate the effect of density-dependent mechanisms, as favourable conditions exist for both foraging adults and survival of young regardless of territorial quality. In times of adverse weather conditions, territorial quality may dictate the productivity of a population by allowing only those pairs occupying high-quality territories to raise young successfully through the increased availability of resources or protection from the elements offered by these higher quality habitats (Newton 1998).

Nest placement and site-specific characteristics of a nest may also affect breeding success, independent of the surrounding quality, by influencing the nest microclimate and the level of protection offered to the young from environmental conditions. A single territory may offer many different breeding locations of differing suitability (Martin
1988). The selection of a nest site in a territory may be unrelated to other aspects of territorial quality and as such could play a large role governing the productivity of a breeding pair, independent of the quality of habitat that is occupied (Ceballos and Donazar 1989). Weather conditions combined with the physical characteristics of the nest site may potentially explain the reproductive variability exhibited by bird populations in greater detail than territorial quality alone.

This study examined habitat quality and its relationship to regulation and patterns of fluctuation exhibited in the reproductive output of a population of Peregrine Falcons (*Falco peregrinus anatum*) in the Yukon Territory, Canada. Specifically, this study tested whether the site-dependent regulation hypothesis explained variation in the productivity of Peregrine Falcons, relative to physical characteristics of the nest-site and weather conditions. Until now, the characteristics of successful Peregrine Falcon territories along the Yukon River and the relationship to habitat quality have not been quantified. A measure of territorial habitat quality was needed to address the hypothesis of site-dependent regulation. I used occupation frequency as a measure of habitat quality (Sergio and Newton 2003) and tested whether differences in the occupation frequencies of territories existed and how the differences were associated with reproductive output of individuals occupying territories.

The main objective of this study was to explain the variation in productivity for this population of Peregrine Falcons using the site-dependent regulation hypothesis. I predicted that there would be identifiable and measurable differences in territorial and nest-site characteristics among territories with different reproductive output and quality. I also determined whether other processes, independent of territory quality, such as
weather and micro-scale nest characteristics, limited this population independent of density (adapted from Rodenhouse et al. 1997).

METHODS

STUDY AREA AND POPULATION

The study area encompassed a 200-km stretch of the Yukon River valley in the western Yukon Territory, Canada, between the mouth of the Stewart River (63° 26' N, 138° 29' W) on the upstream side of Dawson City, and to Sheep Rock near the Alaska border (64° 62' N, 140° 75' W). The community of Dawson City is located in the approximate centre of the study area (64° 03' N, 139° 25' W). Physiographically, the study area occurs within the largely unglaciated, gently sloping Yukon plateau, which is composed mainly of metamorphic limestone substrate (Froese et al. 2001). Elevation of land adjacent to the Yukon River in the study area ranges from 300 m above sea level at the Yukon River to cliff elevations of 650 m. Peregrine Falcons nest on cliff ledges along the river, and there were approximately 50 nesting cliffs known to exist in the area prior to this study (Mossop 2001).

The study area occurs within a semi-arid continental climate, with an average annual precipitation of 324 mm (Scudder 1997). It is within the sub-arctic boreal forest, with major communities of black spruce (*Picea glauca*), mixed spruce-deciduous forest and riparian deciduous woodland (Rowe 1972). In addition, past forest fires (1993, 1998) have left extensive burned areas, consisting of snags and little shrub cover throughout the river valley. A large forest fire burned extensive portions of the river valley in the study area in 2004.
This study population of Peregrine Falcons has been surveyed extensively over the past 30 years (Mossop 1988) and experienced steady population growth since the pesticide-induced population crash of the 1970’s. The breeding population of Peregrine Falcons inhabiting the Yukon River has more than doubled in the past 10 years (D. Mossop, unpubl. data).

MEASURES OF PRODUCTIVITY
Surveys of Peregrine Falcons nesting along the Yukon River were conducted during 8 breeding seasons from 1984 to 2001 (D. Mossop, unpubl. data). I also monitored this population intensively throughout the breeding season (20 May to 31 July) from 2002 to 2004. It was not possible to navigate the river prior to 20 May and so the exact arrival date of breeding pairs in the study area was unknown. Previous research on populations of Peregrine Falcons in adjacent areas of Alaska and Canada has determined that individuals typically arrive near 1 May (Schmutz et al. 1991, Britten 1998), and I assumed that this population exhibited similar patterns.

Preliminary surveys were performed in 2002-2004 to determine territory occupancy, and if nest sites were readily accessible, clutch sizes were recorded (2003 and 2004). Follow-up surveys throughout the breeding season documented hatching dates, and number of fledged young. In all other years (1984-2001) the number of fledged young was also documented (D. Mossop, unpubl. data). A nest was considered successful if at least one young fledged. Reproductive output was defined as the number of young fledged from a territory.
INFLUENCE OF NEST-SITE AND TERRITORIAL CHARACTERISTICS ON PRODUCTION OF YOUNG

To determine the physical features of the nesting cliff important to reproductive output of Peregrine Falcons, I measured nest-site characteristics on accessible ledges during the breeding season of 2003. At each nest site (Appendix I), I documented the presence of an overhang, and measured depth and width of the nest ledge, height of the ledge above the river and accessibility to the ledge site (details below). The height of the ledge and cliff were determined using a GPS altimeter unit, subtracting the altitude at the river. The GPS altimeter was calibrated using known points of elevation.

Potential nest predators such as wolverines (*Gulo gulo*), marmots (*Marmota caligota*) and red foxes (*Vulpes vulpes*) inhabit the region. I used a 5-point scale to estimate ledge-site accessibility. This subjective ranking system approximated the difficulty for a mammalian predator to access the nest. Easily accessed sites were ranked 1, while sites with near impossible entry were ranked 5.

Characteristics of a nest site may exist at a different scale compared to the territory and were therefore tested independently of territorial quality. I used step-wise linear regression to determine how nest-site characteristics influenced the reproductive output of individuals occupying cliffs. Number of young fledged was the dependent continuous variable, while overhang (presence/absence) was entered as a bivariate dummy variable in the model, and river channel width, ledge depth, ledge length, ledge height, ledge aspect, accessibility, and cliff length were continuous variables. The stepwise variable selection method was used to select the variables to include in the model ($\alpha$ to enter < 0.05 and $\alpha$ to remove > 0.10) (Zar 1998). If two or more dependent
variables were significantly correlated, I selected one variable for analysis (based on biological validity) to remove collinearity from the model. All variables must pass the tolerance criterion to be entered in the equation, regardless of the entry method specified. The default tolerance level was set to 0.0001 (Norusis 2000). A variable was not entered if it would cause the tolerance of another variable already in the model to drop below the tolerance criterion. All subsequent multiple regression analyses followed this stepwise procedure.

Attributes of the entire cliff were measured separately from nest-site characteristics, because a single cliff could have multiple nesting ledges. These characteristics (Appendix II) were determined by recording location points using a hand-held GPS unit and uploading these coordinates onto a regional image (2001 Landsat Moasic image). Measurements included perpendicular river channel widths, distance from a nest-site to the next nearest known occupied nest-site, cliff length, cliff aspect and cliff height.

TERRITORIAL QUALITY
Territorial quality was assessed by combining the long-term data set (8 years between 1984-2001; D. Mossop, unpubl. data) with my data set (2002-2004), and using the methods outlined in Sergio and Newton (2003). The frequency of territorial occupation was used as a measure of quality and related to measures of reproductive success (Sergio and Newton 2003). I tested whether territories were occupied non-randomly by comparing the pattern of territorial occupancy to a pattern of random occupancy (Poisson distribution; Zar 1998), and using a Kolmogorov-Smirnov test to determine if occupancy
rates deviated from a random pattern. The coefficient of variation for territorial reproductive output was calculated and was log-transformed to achieve a normal distribution.

The relationship between territorial occupation frequency and both reproductive output and its coefficient of variation were tested using Pearson product-moment correlation \((n = 56\) territories) (Zar 1998). To test whether higher quality territories were occupied earlier in the breeding season, I used a Pearson product-moment correlation to examine the relationship between frequency of territorial occupancy and estimated clutch initiation date (2003 and 2004) (Zar 1998). Clutch initiation date was estimated by subtracting the estimated hatching date of young (determined using photographs of known-age nestlings; Clum et al. 1996) at territories \((n = 41\) territories) by 36 days to account for the incubation and laying period (Court et al. 1988, Bradley et al. 1997). The relationship between occupation frequency of territories and physical characteristics of the cliff (i.e., cliff height, river channel width, cliff aspect, cliff length, nearest neighbour distance; \(n = 44\) territories) was tested with stepwise regression analysis (\(\alpha\) to enter < 0.05 and \(\alpha\) to remove > 0.10; see above) (Zar 1998).

I used a three-level ranking system to rank territorial occupancy as high (occupied > 75\% of the years surveyed), medium (occupied 25 to 75\%) or low (occupancy below 25\%), following Hickey’s (1969) observations of habitat use by Peregrine Falcons. Previous research has shown that the sites that appeared to be of higher quality tend to be always occupied (Ratcliffe 1993), while medium-quality sites show a larger range of occupation history. The ranking system restricts high-quality sites to those occupied most frequently, and low-quality sites to rarely occupied territories. The ranks of occupied
territories in each year were averaged to obtain the overall quality of all territories occupied in a year. To test the site-dependent regulation hypothesis, the temporal patterns of occupancy and population productivity were correlated with mean annual quality using Pearson product-moment correlation (Sergio and Newton 2003, Kruger and Lindstrom 2001, Rodenhouse et al. 1997).

WEATHER
Temperature (°C), visibility (km), wind speed (km / hr) and relative humidity (%) measured hourly, and daily precipitation (mm), were obtained for the period of May 1 to July 31 in all years surveyed, from the Environment Canada weather station near Dawson City, at the center of the study area. In addition, hourly temperature data were gathered from four sites using HOBO data loggers to test for temperature variability within the study area. Temperature probes were placed 35 and 70 km both upstream and downstream of the Environment Canada weather station at Dawson City. Pearson product-moment correlation and paired t-test analyses were used to determine the relationship between temperature at Dawson City and each location with a data logger (Zar 1998).

I divided the breeding season into four intervals to test the influence of weather conditions on the productivity of Peregrine Falcons during each interval separately. These four intervals were: pre-laying (May 1-May 7), egg laying and incubation stage (36 days; May 08-June 13), early nestling stage (young up to 21 days of age; June 14-July 5) and late-nestling stage (young aged 21 days to fledging (~ 46 days); July 6-July 29) (modified from Bradley et al. 1997). The nestling stage was subdivided to determine the effect of
weather before and after thermoregulatory independence of young was achieved (Bradley et al. 1997), and all intervals were based on the average hatching dates of this population (June 14; determined using the breeding data collected from the breeding seasons of 2002 to 2004). Daily averages were calculated for each weather variable, and these mean daily values were then averaged for each breeding interval. To detect if outliers were present in the data, Dixon’s tests were used, and I employed the $r_{22}$ test statistic (details in Sokal and Rolf 1995).

Stepwise linear multiple regression models were built for each breeding interval to determine which variables significantly predicted the productivity of Peregrine Falcons ($\alpha$ to enter < 0.05 and $\alpha$ to remove > 0.10; see above) (Zar 1998). Weather variables during the incubation, early nestling and late nestling intervals were linearly regressed against the mean annual frequency of successful sites and the mean annual number of fledged young ($n = 11$ years).

Because weather prior to egg laying is probably most influential on the number of pairs making the decision to breed (Elkins 1983), weather variables during the pre-laying interval were analysed with the average yearly occupancy rate as the dependent variable ($n = 11$) in a multiple linear regression. Average yearly occupancy rate was expressed as a proportion of the number of pairs occupying territories over the total number of known territories. To minimize the influence of the growing population, yearly occupancy was expressed as the number of territories occupied divided by the total known at that interval.

Statistical significance was set at an $\alpha$ of 0.05 for all non-corrected tests and all means are given ± 1 standard error. Statistical analyses were performed using SPSS v.
Prior to parametric tests, all variables were assessed for normality with Kolmogorov-Smirnov tests and logarithmic transformations were used to achieve normal distributions where necessary. Levene’s tests were used to assess homogeneity of variances for all data prior to analysis (Zar 1998). Outliers in the data were examined using Dixon’s test (Sokal and Rolf 1995).

RESULTS

DIFFERENCES IN TERRITORIAL AND LEDGE SITE SUITABILITY

A higher number of young fledged from nest sites that had greater ledge depth, decreased accessibility, protection from overhanging rock, and that occurred near narrower sections of the river (Fig. 2.1). The general linear regression model with these variables explained 73.8% of the variation observed in the number of fledged young (Table 2.1). All other nesting features that I measured were not related to the reproductive output of Peregrine Falcons breeding along the Yukon River (partial coefficients; $P > 0.10$).

TERRITORIAL OCCUPANCY RELATIVE TO REPRODUCTIVE OUTPUT

The rate of occurrence of territorial occupation by peregrines relative to the Poisson distribution showed that territories were not occupied randomly over the years surveyed (Kolmogorov-Smirnov $Z = 1.42$, $P = 0.04$, $n = 56$). The occupation frequency of a territory was positively correlated with the average number of young produced on a territory in occupied years ($r = 0.47$, $P < 0.001$, $n = 56$), the number of young per successful nest ($r = 0.68$, $P < 0.001$, $n = 56$), the frequency of the territory successfully fledging young ($r = 0.89$, $P < 0.001$, $n = 56$) and the average number of fledged young
FIGURE 2.1. The relationship between the number of offspring that were fledged by cliff-nesting Peregrine Falcons in the Yukon, Canada, and (A) ledge depth, (B) ledge site accessibility (increased scale denotes decreased accessibility, size of circle and number above denotes number of data points), (C) river channel width, and (D) presence of an overhang (number above standard error bars indicates sample size) in 2003.
TABLE 2.1. Factors affecting the number of young fledged from territories of Peregrine Falcons breeding along the Yukon River, Canada, during 2003, as determined by a multiple linear regression.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.18</td>
<td>1</td>
<td>0.18</td>
<td>0.64</td>
<td>0.43</td>
</tr>
<tr>
<td>Accessibility</td>
<td>4.17</td>
<td>1</td>
<td>4.17</td>
<td>14.81</td>
<td>0.001</td>
</tr>
<tr>
<td>Ledge depth</td>
<td>2.27</td>
<td>1</td>
<td>2.27</td>
<td>8.07</td>
<td>0.009</td>
</tr>
<tr>
<td>River channel width</td>
<td>1.92</td>
<td>1</td>
<td>1.92</td>
<td>6.83</td>
<td>0.015</td>
</tr>
<tr>
<td>Overhang presence</td>
<td>2.04</td>
<td>1</td>
<td>2.04</td>
<td>7.23</td>
<td>0.013</td>
</tr>
<tr>
<td>Error</td>
<td>6.76</td>
<td>24</td>
<td>0.28</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>167.00</td>
<td>29</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
from that territory from all years surveyed \((r = 0.88, P < 0.001, n = 56; \text{Fig. 2.2})\).

Increasing rates of territorial occupancy were associated with significantly earlier clutch initiation dates \((r = -0.41, P = 0.01, n = 41)\).

Peregrines nesting in territories that fledged a greater mean number of young exhibited less variation in the number of young produced \((r = -0.82, P < 0.001, n = 55)\). Similarly, as the frequency of territorial occupation increased, the coefficient of variation in the number of fledged young decreased \((r = -0.66, P < 0.001, n = 55; \text{Fig. 2.3})\).

Higher territorial occupancy rates \((R^2 = 0.41)\) were associated with narrower sections of the river and longer cliff sections (Table 2.2). Cliff height, cliff aspect and nearest neighbour distance were not associated with territorial occupation frequency (all \(P > 0.10\)).

SITE-DEPENDENT REGULATION

The average annual quality obtained by averaging the territory rankings, was inversely related to the number of territories occupied, so that as density increased, the average quality of territories used decreased \((r = -0.90, P < 0.001, n = 11; \text{Fig. 2.4})\). The mean annual number of fledged young by breeding falcons increased with higher mean quality of occupied territories \((r = 0.73, P = 0.01, n = 11; \text{Fig. 2.5})\). It is important to note, however, that data from 2004 largely drives this relationship. The relationship becomes non-significant when the 2004 data point is removed from the analysis \((r = 0.49, P = 0.15, n = 10)\).
FIGURE 2.2. Mean territorial reproductive output of Peregrine Falcons nesting along the Yukon River, Canada, in relation to occupation frequency of territories during 11 years between 1984 and 2004.
FIGURE 2.3. The coefficient of variation in the average number of fledged young on a territory relative to the occupation frequency of that territory by Peregrine Falcons along the Yukon River, Canada, during 11 years between 1984 and 2004.
TABLE 2.2. Factors affecting territorial occupancy rates of Peregrine Falcons breeding along the Yukon River, Canada, during 2003 and 2004, as determined by a multiple linear regression.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>$F$</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.55</td>
<td>1</td>
<td>0.55</td>
<td>10.4</td>
<td>0.002</td>
</tr>
<tr>
<td>River channel width</td>
<td>0.49</td>
<td>1</td>
<td>0.49</td>
<td>9.5</td>
<td>0.004</td>
</tr>
<tr>
<td>Cliff length</td>
<td>0.36</td>
<td>1</td>
<td>0.36</td>
<td>6.8</td>
<td>0.013</td>
</tr>
<tr>
<td>Error</td>
<td>2.15</td>
<td>41</td>
<td>0.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>15.72</td>
<td>44</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
FIGURE 2.4. Mean annual quality of occupied territories relative to the number of territories occupied by breeding Peregrine Falcons along the Yukon River, Canada, during 11 years between 1984 and 2004.
FIGURE 2.5. Mean annual productivity relative to quality of occupied territories by Peregrine Falcons breeding along the Yukon River, Canada, during 11 years between 1984 and 2004 (hollow point represents 2004).
INFLUENCE OF WEATHER ON REPRODUCTIVE OUTPUT

Average daily temperature readings from data loggers located throughout the study area were highly correlated with temperatures at the Environment Canada weather station in Dawson City ($r > 0.85$, $P < 0.001$, $n = 55$ for all probes). In addition, paired $t$-tests between each data logger and the Environment Canada weather station showed no significant difference in temperatures ($P > 0.05$ for all comparisons). This suggests that temperature and weather data from Dawson City was representative of my entire study area.

Visibility during the pre-laying period was significantly correlated with the number of pairs occupying territories ($r = 0.67$, $P = 0.02$, $n = 11$; Fig. 2.6), such that years with higher visibility corresponded with increased occupancy rates of known territories. Average temperature, precipitation, wind speed and relative humidity during the pre-laying interval did not significantly influence the number of breeding pairs occupying territories and attempting to breed ($P > 0.10$ for all variables).

No weather variables during the incubation period significantly influenced productivity of Peregrine Falcons ($P > 0.10$). Visibility during the 2004 nestling period, however, was a significant outlier (Dixon's Test; Sokal and Rolf 1995; $t_{22} = 0.76$, $P = 0.001$, $n = 11$), most likely due to the intense forest fire that occurred in the study area. The subsequent removal of 2004 data from the analysis resulted in a significant negative relationship between precipitation during the early nestling period and the frequency of successfully producing at least one young ($r = -0.67$, $P = 0.04$, $n = 10$; Fig. 2.7a), and between precipitation during the late nestling period and mean annual number of fledged young ($r = -0.68$, $P = 0.03$, $n = 10$; Fig. 2.7b). Precipitation during the late nestling
FIGURE 2.6. Rate of territorial occupancy in relation to visibility conditions prior to laying (May 1 - May 10) by Peregrine Falcons breeding along the Yukon River, Canada, during 11 years between 1984 and 2004.
FIGURE 2.7. The (A) rate of successful occupation by breeding Peregrine Falcons during the early nestling period (young < 21 days old), and (B) mean annual number of fledged young during the late nestling period (young > 21 days old), relative to precipitation totals along the Yukon River, Canada, during 11 years between 1984 and 2004 (hollow point represents 2004 datum).
period was not significantly related to the frequency of successful breeding attempts. Temperature, relative humidity and visibility were not significantly related to either mean number of fledged young or frequency of successful territories \((P > 0.10)\). There was a non-significant trend for increasing windspeed to be associated with fewer fledged young \((P = 0.08)\).

Data on precipitation during the late nestling period and mean annual territorial quality were combined in a stepwise linear regression model, in an effort to better explain the variation in mean annual number of fledged young. Territorial quality was the only variable included in the regression model and explained 53.6% of the variation exhibited in the mean annual number of fledged peregrine young \((F_{1,10} = 10.40, P = 0.01)\). Due to the confounding nature of the forest fires in 2004, I also analysed data with this year removed from the data set \((n = 10)\). The stepwise regression model was comprised only of late nestling precipitation and explained 45.7% of the variation in the mean annual fledged young \((F_{1,9} = 6.73, P = 0.03)\).

DISCUSSION

INFLUENCE OF LEDGE-SITE AND CLIFF-SITE CHARACTERISTICS ON PRODUCTIVITY

Cliff ledges that are used as nesting sites differ in many characteristics (e.g., overhang presence, drainage ability, size, height) and sites that offer more protection from environmental factors typically produce more offspring than sites lacking these characteristics (Mearns and Newton 1988, Olsen and Olsen 1989a). In this study, more young fledged from nest sites that were protected from the environment (Fig. 2.1).
Specifically the presence of an overhang, adequate ledge depth and decreased accessibility (Fig. 2.1 a, b, d) were important aspects of breeding habitat for Peregrine Falcons. The characteristics of nesting habitats used by breeding Peregrine Falcons can be highly variable (Hunt 1988) and the relationship with reproductive output appears to vary among localities, but most studies have reached similar conclusions regarding the importance of protection from the environment in determining reproductive success (Mearns and Newton 1988, Olsen and Olsen 1988, Court et al. 1988). To my knowledge, however, this is the first study to correlate the importance of ledge size on the production of young by Peregrine Falcons. It may be that narrower ledges are more precarious for young birds and falling deaths may be more prevalent on narrower ledges, resulting in fewer young fledging from these sites.

Increased productivity occurred at nesting ledges that were located on narrower river channels (Fig. 2.1c). Decreased river channel width may act to facilitate prey capture by increasing hunting efficiency. Peregrines forage from nesting cliffs (B. Boukall, pers. obs.) and narrower river widths could facilitate prey capture by reducing the air space between falcon and prey and thus the escape paths of potential prey. In addition, foraging peregrines may have a greater element of surprise on narrower sections of the river, increasing hunting efficiency compared to wider sections of the river. Prey may also be less likely to cross large, open gaps at wider sections of the river. Prey recognition by peregrines is an important aspect of their hunting success and efficiency, and prey may be more recognizable in a narrower section of the river (Ratcliffe 1993). The distance involved in prey capture over the river would be considerably less, and prey
capture and retrieval could conceivably be more energy-efficient, especially for larger prey items like waterfowl.

The majority of research on nesting habits of Peregrine Falcons has shown that ledge height is a significant factor influencing the productivity of a nest (Mearns and Newton 1988). In comparison to many of these studies, however, this population is relatively remote with little human disturbance and few predators. Studies in remote locations have shown that Peregrine Falcons tend to nest on lower, more accessible cliffs than those nesting in areas with higher frequencies of disturbance (Court et al. 1988, Ratcliffe 1993). As a result of the remote location of the study area, the height of the ledge appeared to have little impact on the accessibility of the ledge to mammalian predators (including humans), and thus was not an important characteristic of productive nesting sites.

TERRITORIAL QUALITY AND ASSOCIATED HABITAT CHARACTERISTICS

The results of this study provide additional support for the use of territorial occupancy as a measure of habitat quality (Sergio and Newton 2003). Higher frequencies of occupation were strongly correlated with increased average reproductive output from a site (Fig. 2.2). Intraspecific competition for breeding territories within a population has been reported for many bird species (see review in Newton 1998) and follows the despotic ideal-free distribution model (Fretwell and Lucas 1970). Assuming that peregrines adhere to despotic settlement patterns, younger and/or poorer quality breeders will be forced to occupy lower quality sites due to competitive pressures. This would help explain the lowered reproductive output of these sites. Eurasian Kestrels (Falco tinnunculus) arriving
later at the breeding grounds tend to be younger and more inexperienced compared to those individuals arriving earlier (Village 1985). Ferrer and Bisson (2003) found that immature pairs of Spanish Imperial Eagles (Aquila adalberti) more frequently occupied low-quality territories. There was no evidence, however, for age-related differences in reproductive performance after the effect of territorial quality was removed (Ferrer and Bisson 2003). Age-specific (individual quality) and territorial quality effects on the productivity of Peregrine Falcons could not be separated in this study. These two variables, however, can be viewed as being on the same continuum of reproductive response to habitat quality. The influence of parental quality can be additive to the effect of territorial quality, thus exacerbating the differences in production between higher quality sites and those of lesser quality (Sergio and Newton 2003).

A high proportion of young produced from a small number of high-quality territories raises the possibility of phenotypic selection for individuals that choose higher quality habitat (Sergio et al. 2003), assuming that local recruitment occurs in this population (Court et al. 1988). Although post-fledging survival of young was not measured in this study, there is a high probability that the majority of individuals in the next generation will be produced from higher quality territories (Sergio and Newton 2003). Studies on nesting behaviour of a variety of bird species have focused on the benefits of high-quality nest sites and provided evidence for adaptive selection in nest-choice behaviour (Clark and Shutler 1999, Sergio et al. 2003). Studies focusing on genetically distinguishing individuals on the basis of their nest choice behaviour and subsequent fecundity would provide support for adaptive, phenotypic selection of nesting habitat (Sergio et al. 2003).
In this study, highly occupied territories were located on longer cliffs at narrower sections of the river. As with width of the river, longer cliffs may contribute to reproductive output by increasing hunting efficiency and access to prey. The mechanism by which the length of cliff influences the reproductive output of Peregrine Falcons is most likely associated with an increased number of perches from which to hunt. Breeding Peregrine Falcons tend to employ perch-hunting behaviours (Cade 1982, Jenkins 1995), presumably to reduce energy expenditure. Conceivably, a greater number of perch sites could lead to an increased selection of prey targets and hunting tactics, resulting in increased hunting success (Jenkins 2000). Additionally, increased cliff length is associated with decreased vegetation (B. Boukall, pers. obs.), and thus less escape cover for prey species.

Crowding and territoriality mechanisms as represented by nearest known neighbour distance did not have a significant influence on the number of fledged young from a site. These processes probably influence productivity at a small, local scale between two closely occupied sites (Rodenhouse et al. 2003). Although it is possible that interactions occurred between territorial pairs in my study and birds from unidentified sites, this seems unlikely. A large amount of time was spent each year identifying breeding locations along the river valley and the possibility that territories went undetected is considered to be low in this study.

INFLUENCE OF VISIBILITY AND PRECIPITATION ON REPRODUCTIVE OUTPUT
The influence of weather conditions during the pre-laying period and the energy needed for breeding has been intensively examined in birds (Hogstedt 1981, Newton and Marquiss 1981, Korpimäki 1989, see review in Newton 1998). Weather conditions during the preceding winter and spring have been shown to have a large effect on the density of some breeding populations of raptors (Village 1990). Reduced visibility could lower the fitness of potential breeders by decreasing prey availability and accessibility, thus resulting in a reduction in the number of pairs breeding. For example, spring conditions influenced the visibility of potential food sources for foraging Bearded Vultures (Gypaetus barbatus) and had a significant influence on annual breeding densities in the Pyrenees of Spain (Donazar et al. 1993). Similarly, I found that visibility had a large influence on the numbers and success of Peregrine Falcons breeding in the Yukon (Fig. 2.6), probably by mediating foraging conditions. The actual values for visibility presented in Fig. 2.6 (ranging from 27 km to 32 km) are unlikely to be directly related to foraging success of peregrines. Rather, these values more likely represent an index of visibility conditions, with lower values representing those years with many days of poor visibility. Additionally, lower visibility may have had a pronounced effect on the behaviour and numbers of prey occupying the river valleys in the western boreal zone (Jarvinen and Vaisanen 1984). This study is one of the few to document weather influences on the rate of territory occupation by Peregrine Falcons, and implicates the importance of food availability for the occupation of breeding territories.

Several studies on raptors have suggested that heavy rainfall near the time of hatching resulted in mortality of young directly from cold, and indirectly from starvation due to decreased hunting efficiency of parents and increased energetic demands of young.
(Ridpath and Brooker 1985, Mearns and Newton 1988, Olsen and Olsen 1989b, Norriss 1995, Bradley et al. 1997). Increased rainfall during the period when young are unable to independently thermoregulate (Enderson et al. 1972, Bradley et al. 1997) resulted in a decreased number of breeding pairs successfully fledging young in this population of Peregrine Falcons breeding along the Yukon River (Fig. 2.7a). My results support previous research that rainfall during this period is a strong determinant of productivity in Peregrine Falcons (Mearns and Newton 1988); however, precipitation after the period of thermoregulatory independence (young ≥ 21 days old) also significantly influenced the mean number of fledged young each year (Fig. 2.7b). Nestling mortality can arise from both direct and indirect effects of weather, but the majority of research has implicated indirect effects, such as starvation, as being the most important (Siikimäki 1996, Dawson and Bortolotti 2000). Bradley et al. (1997) reported that extended periods of poor weather conditions resulted in increased mortality of nestling Peregrine Falcons. The increased energetic requirements of older and larger young (≥ 21 days) during periods of rapid growth (Boulet et al. 2001) can explain the influence of precipitation on fledgling numbers. Dawson and Bortolotti (2000) suggested that productivity of American Kestrels (Falco sparverius) was limited by availability of food, which was mediated through variation in weather. It would appear that weather-mediated food availability has an effect on the number of Peregrine Falcons fledging from territories in the Yukon.

REPRODUCTIVE VARIATION EXPLAINED BY SITE-DEPENDENT REGULATION
Consistent with site-dependent regulation, the average quality of occupied territories decreased with increasing density of occupied territories in my population of peregrines (Fig. 2.4), followed by a subsequent decrease in mean annual reproductive output of the population. According to the site-dependent regulation hypothesis, the use of progressively less-suitable sites by a growing population should reduce the average productivity for the population as a whole (Rodenhouse et al. 1997). The relationship between productivity and territorial quality was strongly influenced by low productivity and low territorial quality in 2004. Forest fires and poor visibility were prevalent for a large portion of the breeding season, and may have also contributed to the low rate of observed productivity. It would appear that stochastic events like forest fires may strengthen the influence of habitat quality on productivity. The increased density of breeding pairs in 2004 and the subsequent decrease in the quality of occupied territories was associated with a dramatic decrease in the mean number of fledged young. The majority of the fledged young in 2004 were from higher quality territories. The removal of 2004 data from the analysis resulted in a non-significant association between yearly productivity and habitat quality. As a result, the range of variation present in territorial quality was not large enough to detect the process of site-dependent regulation in this population because productivity appears to be also influenced by other factors in the environment, such as fire and precipitation.

SITE-DEPENDENT REGULATION: A QUESTION OF SCALE?

The effect of ledge-site characteristics, weather conditions and territorial quality on productivity of Peregrine Falcons implies that population regulation can occur by mechanisms operating at both the larger regional scale and the scale of the nest site.
Although territorial quality can be an important determinant of reproductive success, it is possible that nest-site selection by individuals may act to decouple this density-dependent mechanism to some degree. The young of many raptor species may imprint on their natal sites, and consequently choose similar sites when breeding age is reached (Temple 1977). Young that fledge from higher quality territories may return as breeders and nest in poorer quality territories, but select nest sites that offer increased benefits, regardless of surrounding habitat quality. The characteristics of the nest ledge, for example, can alleviate effects of weather by offering protection from the elements to nestlings, reducing their energy expenditure (Newton 1998). In addition, good weather (low precipitation) during the late nestling period may act to decouple the relationship between mean reproductive output and territorial quality by allowing breeders in low-quality territories to successfully fledge young.

Good-quality nesting habitat has been shown to mitigate the influence of poor weather conditions on the development and growth of young in other bird species (see review in Newton 1998). Studies have shown that Peregrine Falcons breeding in better sites are capable of successfully fledging young, even in years with poor weather conditions (Olsen and Olsen 1989a). Therefore, the combined influence of precipitation and territorial quality should explain more variation in mean annual fledged young than either factor alone. Territorial quality, however, was the only significant factor in the model explaining variation in the mean annual number of fledged young when all years were considered. When the datum for 2004 was removed from the analysis, precipitation during the late nestling interval accounted for a portion of the variation in yearly mean number of fledged young ($R^2 = 0.46$), whereas territorial quality was not a significant
influence. The difference between analyses with and without 2004 illustrates the large
influence that stochastic events like forest fires can have on productivity of a population.
The forest fire of 2004 appeared to amplify the effect that territorial quality has on
productivity as more young fledged at sites of higher quality. These results may be
partially driven by differences in food availability between territories, and future research
should examine differences in occupancy and food availability between burned and
unburned sites, and the relationship with reproductive success of Peregrine Falcons. It
should be noted that both of my models were fit using a relatively small sample ($n = 11$
and 10), and more data are required to increase the power of such models to explain
productivity in Peregrine Falcons.

CONCLUSION

In conclusion, the hypothesis of site-dependent regulation was, to some extent, supported
in this population of Peregrine Falcons. Weather conditions, namely precipitation during
the nestling period, also have a large influence on population dynamics. Implications of
this finding are extremely important in northern populations, where the climate appears to
be rapidly changing (Hebda 1997). Alteration in precipitation conditions, especially
during the month of July when young have large energetic requirements, coupled with
reductions in territorial quality, could have important implications for the population
dynamics of Peregrine Falcons. Future research should concentrate on whether territorial
quality remains consistent relative to changing environmental conditions (i.e., effect of
forest fires on long-term territorial quality). Additionally, to further our understanding of
how mechanisms of regulation influence population dynamics, research needs to separate the influences of habitat quality and individual quality on the production of young.

The use of territorial occupancy as a measure of quality has important implications for the monitoring and management of avian populations. Rather than complete surveys, which tend to be intensive, time-consuming protocols, it may be possible to examine fewer numbers of medium to high-quality territories to gain information about the dynamics and health of a population. Owing to weather conditions and the characteristics of the individuals occupying medium-quality nest sites, more variation in reproductive output among years should be exhibited at these sites. Concentrating survey efforts on these medium-quality territories should provide insight into the variability present in productivity of the population as a whole from year to year.

The dynamics of populations are influenced by multiple environmental factors at multiple scales. An understanding of how these factors interrelate is crucial for the conservation of populations in the now rapidly changing environment. The behaviour and experience of individuals can either act in concert or antagonistic to the site-dependent hypothesis. The knowledge of how individuals select sites at different scales (nest site, territorial, population, regional), coupled with the genetic makeup of individuals in the populations, will further our understanding of how site-dependent regulation mechanisms operate in the environment with respect to natural selection.
3. INFLUENCE OF PREY USE AND SELECTION ON REPRODUCTION BY PEREGRINE FALCONS BREEDING ALONG THE YUKON RIVER

INTRODUCTION

Food availability often determines the survival and reproductive output of organisms (Sutherland 1996), and many studies of bird populations have indicated that variable food supplies act to limit productivity (Hogstedt 1981, Martin 1987, Korpimäki 1989). The production of larger broods requires frequent and efficient foraging by parents to sustain the nutritional requirements of the developing nestlings (Martin 1987, Deerenberg et al. 1995). Due to variability in the environment, parents may not be able to meet the energetic demands of the young and nestling mortality often results with larger brood sizes (see review in Newton 1998). Subsequently, variability of food in the environment can not only limit productivity, but can also determine the demographics of avian populations (Newton 1998).

Birds of prey can take prey either in accordance to its abundance (opportunistic feeders; Sodhi and Oliphant 1993, Village 1982) or select prey in relation to its profitability (Hunter et al. 1988, Steenhof and Kochert 1988). Different prey types will differ markedly in their biomass and potential for energy yield, and the effort involved in obtaining prey can be as important as the energetic value of the prey (Suryan et al. 2000). Individual differences in foraging ability and prey selection among breeding pairs can result in differences in feeding patterns and reproductive output (Newton 1976, Newton and Marquiss 1982, Palmer et al. 2004). Foraging adults should select for prey types in the landscape that are most energetically profitable, for both the young and parents.
Energetically profitable prey types are those for which the difference between the costs of procurement and the energetic yield are maximized. Birds that are optimal foragers are described as selective feeders (Jaksic 1989). If selected prey types decline sufficiently such that foraging efficiency is significantly lowered, then less-profitable prey types will become increasingly important, resulting in the expansion of diet breadth (Stephens and Krebs 1986). Lowered foraging efficiency by a breeding adult and the subsequent expansion of diet breadth, should result in lowered reproductive output (Stephens and Krebs 1986).

This study examined the relationships between productivity and the use, abundance and selection of prey by individual pairs of Peregrine Falcons (*Falco peregrinus anatum*) breeding along the Yukon River, Yukon Territory, Canada. I estimated prey abundance on individual territories and compared these indices to prey use and productivity at a nesting territory. Peregrine Falcons are described as predominantly avian predators that use a wide range of prey items, from passerines and waterfowl to other raptors (Ratcliffe 1993, Newton 1979). Peregrine Falcons appear to use certain prey resources disproportionately to their availability (Hunter et al. 1988, Rosenfield et al. 1995) and the selective feeding of peregrines could result in variable reproductive output based on the prey selection of individual breeding pairs. Apart from studies by Wiebe and Bortolotti (1992, 1994, 1995) and Dawson and Bortolotti (2000), few studies have examined the influence of food supply on productivity on a per-territory basis (Thomas and Taylor 1990).

This study had three main objectives. The first was to describe the diet of breeding Peregrine Falcons in the Yukon Territory, examining diet diversity and prey
biomass among sites of differing productivity. I expected both average prey biomass and biomass per nestling to increase with increasing brood size.

Secondly, I wanted to determine whether breeding Peregrine Falcons in the Yukon are selective feeders. If Peregrine Falcons are not selective in their prey use, then they should use prey species relative to their abundance in the environment and reproductive output should be related to the overall abundance of prey within their territory. The alternative is that Peregrine Falcons are selective predators and choose prey based either on relative profitability or abundance. Peregrines should take prey according to its relative efficiency (e.g., abundance, biomass) and feed more selectively when profitable prey species are abundant (Stephens and Krebs 1986).

Finally, I examined the differences among territories in terms of abundance of selected prey types to determine if relationships existed that would explain variation in productivity among different territories. If prey types that were preferentially selected were abundant, I predicted an increase in reproductive output and subsequent decrease in diet diversity of breeding Peregrine Falcons.

METHODS

STUDY AREA

The study area encompassed a 200-km stretch of the Yukon River valley in the western Yukon Territory, Canada, between the mouth of the Stewart River (63° 26’ N 138° 29’ W) on the upstream side of Dawson City, and to Sheep Rock near the Alaska border (64° 62’ N 140° 75’ W). Peregrine Falcons nest on cliff ledges along the river, and there were approximately 50 nesting cliffs known to exist in the area prior to this study (Mossop
2001). The study area occurs within the sub-arctic boreal forest, with major communities of black spruce (*Picea glauca*) forest, mixed spruce-deciduous forest and riparian deciduous woodland (Rowe 1972). Past forest fires (1993, 1998) have left extensive burned areas, consisting of snags and little shrub cover throughout the river valley. A large forest fire burned extensive portions of the river valley in the study area in 2004.

Occupied breeding territories of Peregrine Falcons were identified in late May and successful territories (≥ 1 fledged young) were identified in July. The number of young fledged (0, 1, 2, 3 young) from each territory was recorded. Prey abundance and selection by Peregrine Falcons nesting in the study area were assessed for 15 randomly selected occupied territories: 6 in 2003 and 9 in 2004.

**PREY ABUNDANCE**

To quantify relative indices of territorial prey abundance, two avian prey counts were conducted approximately two weeks apart in the foraging area of each territory during the breeding seasons of Peregrine Falcons in 2003 and 2004 (June 1-June 30). In each foraging area, the two counts consisted of two 1250-m terrestrial transects perpendicular to the river, each located 1 km (upstream and downstream) from the nest on the opposite shore, and one river transect of 2 km.

Counts began at 04:00 and finished by 08:00. Variable circular-width point counts (Reynolds et al. 1980) were located every 250 m along the terrestrial transects. The initial point count began 100 m from the river shore and a total of 6 points were sampled on each terrestrial transect. Each point count was a total of 6 minutes in duration, and began 1 minute after arriving at the point. All birds encountered between the points were
recorded and their distances and angles away from the transect estimated, so as not to
duplicate individuals recorded. The riverine transect was censused from a drifting boat in
each nesting territory to determine the relative abundance of birds in riverine / riparian
area (Hunter et al. 1988). Riverine counts were conducted immediately following
terrestrial counts at each territory, beginning at 08:00 and finishing by 09:00. River
transects began 1 km upriver of the nest site and ended 1 km past the nest, and all birds
seen or heard on one side of the river were counted. The area sampled during my surveys
was therefore well within the radius of 3 km where the majority of foraging flights by
Peregrine Falcons occur (Beebe 1974, Bird and Aubry 1982, Enderson and Kirvin 1983,
Britten 1998).

PREY USE

Prey use was determined from prey remains (Errington 1932, Oro and Tella 1995)
collected from a total of 13 and 12 nest sites in 2003 and 2004, respectively. Each nest
was analysed separately. Prey remains were collected from nesting ledges in mid-July of
each year, when the young were approximately 30-40 days of age. Data from pellet
examinations were not included in the analysis because pellets could not be found or
collected at all ledges. Also, examination of pellets produced by bird-eating raptors
generally yields few identifiable remains (Redpath et al. 2001). At each site, efforts were
made to gather all prey remains in the vicinity of the nest, including directly below ledge
and all accessible perches.

Prey remains were identified by comparing feathers, wings, feet, skulls, and other
anatomical features with specimens from the University of Northern British Columbia
and University of Alberta museum collections. Remains were identified to species, except for thrushes, which were identified to genus (*Catharus*), and scaup species (*Aythya affinis* and *A. marila*) which were each pooled. I identified the minimum number of individuals present in prey remains based on the most commonly found bone or body part representing one individual (Poole and Boag 1988). Preliminary analyses revealed that mammalian prey items (*Tamiasciurus hudsonicus, Microtus spp.*, *Peromyscus maniculatus*) occurred in the prey remains collected from nesting ledges of Peregrine Falcons. These mammalian prey remains, however, constituted a small percentage of the total prey (1.3%) and were thus excluded from further analysis.

To provide a coarse measure of the composition of prey utilized by breeding Peregrine Falcons, I estimated biomass for all prey items identified to species, using data found in Dunning (1993). Biomass of each sex was averaged for species that were sexually dimorphic in size. Prey remains were then separated into 5 biomass classes [small (< 50 g), midsize (51-250 g), medium (251-500 g), mid-large (500-1000 g) and large (> 1000 g)] to examine the use of different-sized prey items for each territory. Small passerines, sparrows, and the majority of finches were placed into the small biomass class (< 50 g), shorebirds, thrushes and jays, woodpeckers and waxwings into the mid-size biomass class (51-250 g), while waterbirds, gulls and other birds composed the majority of the medium (251-500 g), large (501-1000 g) and heavy (> 1000 g) biomass classes.

Prey remains were also separated into 10 prey classes on the basis of both taxonomic (Family) and habitat associations (i.e., waterbirds includes ducks, geese, and grebes). The 10 prey classes representing all species were: shorebirds, waterbirds, woodpeckers, thrushes and jays, finches, sparrows, small passerines, waxwings, gulls,
and other birds, which included raptors (Falconiformes), owls (Strigidae), ravens (Corvidae) and grouse (Phasianidae). The thrushes and jays prey class also included Rusty Blackbirds (*Euphagus carolinus*), because of their similar size and habitat associations (spruce-dominated). Warblers, flycatchers, and other small passerines (< 25 g) were combined into small passerines, also based on relatively similar size and habitat associations. The other birds prey group was formed to account for species that were present in small numbers and not included in other classes.

I tested for annual differences in prey usage in two ways. Mann-Whitney *U* tests (Zar 1998) were used to test whether differences in the ranks of both the 5 biomass classes and 10 prey classes occurred between years. A chi-square test of heterogeneity was use to test whether the frequency of prey usage of the 5 biomass classes and 10 prey classes occurred between years.

**SELECTION ANALYSIS**

I used compositional analyses (Aitchison 1986, Aebischer et al. 1993) to test for individual selection or avoidance of prey types in terms of biomass and prey class. Compositional analysis is commonly employed to determine whether individual organisms exhibit selection for particular prey or habitat type by comparing proportional use to availability. Compositional analysis uses log-ratio transformations to remove the interdependence of proportional numbers in the dataset. The analysis produces a multivariate matrix with \( X \) number of rows and columns (\( X \) equals the number of prey types), where each component of the matrix is the log-ratio of availability of a resource subtracted from a log-ratio of resource use, for each animal. A ranking of resource types
from ‘most selected’ to ‘least selected’ can be calculated from this matrix and individual components in the matrix can be averaged and their standard errors used to determine where nonrandom use occurs. A value of 0.01 was used to replace any prey items not detected in either the abundance indices nor the prey remains. This approach allows for design 3 multivariate analyses (Aitchinson 1986, Aebischer et al. 1993).

Selection or avoidance of a prey group was determined by examining whether the selection ratios included 0 in the 95% confidence limits of each element, thus showing either significant selection (ratio > 0) or avoidance (ratio < 0). The prey selection of breeding Peregrine Falcons was examined for the 5 biomass classes and 10 prey classes. Bonferroni corrections were used to account for the multiple comparisons between the different biomass and prey classes (α = 0.01 and α = 0.005, respectively). Prey selections were determined from each territory after pooling both years of study (2003 and 2004) to ensure adequate sample size for the analysis (n = 15) (Aebischer et al. 1993).

PRODUCTIVITY RELATIONSHIPS WITH PREY

Levins’ diet diversity measure was calculated for the prey classes used by breeding Peregrine Falcons, using the formula: 

\[ B = 1 / \sum p_i^2 \]

where \( p_i \) is the proportion of prey class \( i \) in the diet (Levins 1968). Diversity was then standardized to a scale of 0 to 1, using Hulbert’s (1971) equation: 

\[ B_s = (B-1) / (n-1) \]

where \( B \) is Levins’ diversity measure and \( n \) is the number of categories (\( n = 10 \) prey classes). Indices of diet diversity were calculated using the prey classes for each territory with collected prey remains.

I used 2-way random-factor ANOVA to test for differences in the mean prey biomass and mean prey biomass per nestling among territories of differing reproductive
output \((n = 25\) territories) and between years. Brood size \((1, 2, 3\) young) was the fixed categorical independent variable. Bonferroni post-hoc tests were then used to determine where significant differences in the mean prey biomass among brood sizes occurred.

I tested for differences in diet diversity among sites of differing productivity with an ANCOVA random-effects model (Zar 1998). Due to the influence of increased number of prey items on diet diversity, the number of prey items was used as a covariate \((n = 25\) territories) and the number of fledged young \((1, 2, 3\) young) as the categorical independent variable. Data were plotted to confirm linear relationships between prey items and diet diversity. Regression coefficients were assumed to be homogenous if the interaction term between the independent variable and the covariate was non-significant \((P > 0.05)\). Bonferroni post-hoc tests were used to determine where significant differences in the diet diversity among brood sizes occurred.

To examine the relationship between prey abundance and reproductive output on individual territories \((n = 15\) territories), a Kruskal-Wallis test was performed due to the ordinal nature of the data. I compared the proportions of each prey type for the different number of fledged young \((0\) to \(3\) young). Proportions were used instead of raw scores to control for the potentially confounding effect of prey count numbers on the response variable.

Statistical significance was set at an \(\alpha\) of 0.05 and all means are given \(\pm 1\) standard error. In cases where a territory was sampled in both years, only one year was used in statistical analyses to avoid pseudoreplication. Statistical analyses were performed using SPSS v. 11.0 (Norusis 2000) and SAS (SAS Institute 1997) software. Kolmogorov-Smirnov tests were used to confirm normality and Levene’s tests were used
to test for homogeneity of variances for all data analyzed with parametric statistical tests (Zar 1998).

RESULTS

PREY USE

In 2003 and 2004, 255 individuals of 35 species and 324 individuals of 45 species, respectively, were identified from the prey remains collected at nesting ledges (2003: \( n = 15 \), 2004: \( n = 18 \); see Appendix III). Thirty-four species were recorded in both years, and 10 species were recorded in 2004 that were not recorded in 2003. Single specimens represented the 10 species not recorded in 2003. The American Robin (\( Turdus migratorius \)) was the most frequently used prey item in both 2003 (8.2%) and 2004 (9.6%). The five most frequently used prey species (American Robin, Gray Jay (\( Perisoreus Canadensis \)), Dark-eyed Junco (\( Junco hyemalis \)), Varied Thrush (\( Ixoreus naevius \)) and Catharus thrushes [Swainson’s (\( C. ustulatus \)), Gray-cheeked (\( C. minimus \)) and Hermit (\( C. guttatus \))] did not differ significantly between years (\( \chi^2 = 1.2, P = 0.88 \)).

The prey classes that were used most frequently in 2003 and 2004 were the thrushes and jays (29.8 and 28.1%) followed by waterbirds (18.8 and 12.7%) (Table 3.1). The rank order of the percentage of prey classes used did not differ significantly between years (\( U = 55, n = 10, P = 0.35 \)).

The Waterbird prey class accounted for the majority of prey biomass brought to the nesting ledge in both years (58.0% and 59.8%; Table 3.1). Heavier birds such as scaup species, Northern Shoveler (\( Anas clypeata \)) and American Wigeon (\( Anas \))
TABLE 3.1. Percent frequency and biomass of prey classes used by Peregrine Falcons breeding along the Yukon River, Yukon Territory, Canada, from 2003 and 2004.

<table>
<thead>
<tr>
<th>Prey class</th>
<th>2003</th>
<th></th>
<th></th>
<th>2004</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>% frequency</td>
<td>% biomass</td>
<td>n</td>
<td>% frequency</td>
<td>% biomass</td>
</tr>
<tr>
<td>Waterbirds</td>
<td>48</td>
<td>18.8</td>
<td>58.0</td>
<td>41</td>
<td>12.7</td>
<td>59.8</td>
</tr>
<tr>
<td>Woodpeckers</td>
<td>15</td>
<td>5.9</td>
<td>2.9</td>
<td>21</td>
<td>6.5</td>
<td>4.8</td>
</tr>
<tr>
<td>Thrushes &amp; jays</td>
<td>76</td>
<td>29.8</td>
<td>8.3</td>
<td>91</td>
<td>28.1</td>
<td>11.4</td>
</tr>
<tr>
<td>Finches</td>
<td>13</td>
<td>5.1</td>
<td>0.6</td>
<td>30</td>
<td>9.3</td>
<td>1.5</td>
</tr>
<tr>
<td>Sparrows</td>
<td>20</td>
<td>7.8</td>
<td>0.7</td>
<td>35</td>
<td>10.8</td>
<td>1.6</td>
</tr>
<tr>
<td>Small passerines</td>
<td>12</td>
<td>4.7</td>
<td>0.2</td>
<td>31</td>
<td>9.6</td>
<td>0.7</td>
</tr>
<tr>
<td>Waxwings</td>
<td>13</td>
<td>5.1</td>
<td>1.2</td>
<td>13</td>
<td>4.0</td>
<td>1.4</td>
</tr>
<tr>
<td>Others(^a)</td>
<td>22</td>
<td>8.6</td>
<td>9.9</td>
<td>17</td>
<td>5.2</td>
<td>7.8</td>
</tr>
<tr>
<td>Gulls</td>
<td>11</td>
<td>4.3</td>
<td>14.9</td>
<td>5</td>
<td>1.5</td>
<td>5.5</td>
</tr>
</tbody>
</table>

\(^a\) Other birds includes raptors, ravens and grouse
were taken much less frequently, but contributed greatly to the biomass accumulated.

Prey used was divided into 5 biomass classes and compared between years (Fig. 3.1). The rank order of prey biomass use did not differ between years ($U = 10$, $n = 5$, $P = 0.34$), but the frequency of each biomass class that was used differed significantly between years ($\chi^2_4 = 20.4$, $P < 0.001$), with the < 50 g class contributing largely to this difference ($\chi^2_1 = 20.3$, $P < 0.001$).

PREY AVAILABILITY AND SELECTION

The two prey counts conducted on each territory did not differ significantly from each other in terms of abundance for each species observed (Wilcoxon signed-ranks test, $P > 0.15$). The numbers of prey observed were therefore averaged between the two prey counts to provide an overall index of prey abundance for each territory and subsequently divided into the same prey and biomass classes as was done for prey remains.

During counts of territorial prey abundance, 2399 individuals belonging to 69 species were identified in 2003, and 2279 individuals of 63 species were identified in 2004. Prey species weighing less than 50 g were the most commonly encountered birds in each territory. Pooling the data from all years and territories showed that sparrows (Emberizidae) were the most abundant prey group accounting for 25.2% of the total detections, followed by the thrushes and jays class (21.4%). It should be noted that in 2003, higher numbers of Common Redpolls (Carduelis flammea) and White-winged Crossbills (Loxia leucoptera) were observed on territories, presumably due to mast
FIGURE 3.1. Use of different biomass prey classes (± 95% CI) by Peregrine Falcons breeding along the Yukon River, Canada, in 2003 (n = 16 sites) and 2004 (n = 18 sites).
production of spruce cones in the region. Breeding Peregrine Falcons showed non-
random selection of prey both in terms of biomass ($\lambda = 0.030, \chi^2 = 52.74, P < 0.001$) and
prey class ($\lambda = 0.049, \chi^2 = 45.23, P < 0.001$).

The compositional matrix ranked the selection of prey items by biomass in the
order: 251 to 500 g > 51 to 250 g > 501 to 1000 g > less than 50 g > more than 1000 g
(Fig. 3.2). There were no detectable differences in the use among all biomass types. The
biomass class with the highest use did not correspond with the most available biomass
class (Fig. 3.2). Prey items weighing more than 1000 g were avoided when compared to
the other biomass classes (Fig. 3.3).

The shorebird, waterbird, woodpecker, thrushes and jays, waxwing, gulls and
other bird prey classes tended to be used by foraging peregrines greater than their
availability (Fig. 3.4), whereas sparrows, finches and small passerines were avoided. The
compositional matrix ranked the selection of prey items by prey classes in the order:
waterbirds > shorebirds > woodpeckers > thrushes and jays > finches > other birds >
waxwings > gulls > small passerines > sparrows. Shorebirds and waterbirds were
significantly selected whereas sparrows were avoided by foraging Peregrine Falcons (Fig.
3.5). Detectable differences existed between the two top-ranking prey classes (waterbirds
and shorebirds) and the two lowest-ranking classed (sparrows and small passerines).

INFLUENCES ON PRODUCTIVITY

There were large differences in the productivity of the peregrine population between
2003 and 2004, with a significantly higher frequency of nests fledging young in 2003 (74
young) than in 2004 (41 young) ($\chi^2 = 9.47, P < 0.01$). The mean reproductive output of
FIGURE 3.2. Availability and use of biomass classes (± 95% CI) by breeding Peregrine Falcons (2003 and 2004) along the Yukon River, Canada. Prey availability was determined from the average number of prey species surveyed in two prey counts.
FIGURE 3.3. Selection coefficients ± 99% CI (i.e., Bonferroni-corrected 95% CI) of biomass classes for Peregrine Falcons breeding along the Yukon River, Canada, from 2003 and 2004. Confidence intervals that do not overlap with 0 indicate either significant selection (selection coefficient > 0) or avoidance (selection coefficient < 0).
FIGURE 3.4. Availability and use of prey classes (± 95% CI) by breeding Peregrine Falcons (2003 and 2004) along the Yukon River, Canada. Prey availability was determined from the average number of prey species surveyed in two prey counts in each year.
FIGURE 3.5. Selection coefficients ± 99.5% (i.e., Bonferroni-corrected 95% CI) of prey classes used by Peregrine Falcons breeding along the Yukon River, Canada, from 2003 and 2004. Confidence intervals that do not overlap with 0 indicate either significant selection (selection coefficient > 0) or avoidance (selection coefficient < 0).
territories sampled for prey abundance was 2.33 young in 2003 (n = 6 territories) and 0.78 young in 2004 (n = 9 territories); these differences in reproductive output between years approached significance (U = 11.5, P = 0.07, n = 15). Increased brood sizes in territories were associated with higher mean prey biomass present at ledges (Fig. 3.6), as nest sites (n = 25) that fledged a greater number of young had significantly higher prey biomass (Table 3.2). There was no significant effect of year on this relationship nor was there an interaction between year and prey biomass (Table 3.2). Bonferroni post-hoc comparisons showed that significant increases in the mean prey biomass collected from the nesting ledge occurred as the number of young increased for all brood sizes (1, 2, 3 young; all P values < 0.01).

Increased brood size resulted in significantly lowered mean biomass per nestling (Table 3.3). Bonferroni post-hoc comparisons showed that territories with one young received significantly higher amounts of food per nestling than territories with 2 or 3 young (P < 0.01), while prey biomass per nestling was not significantly different between broods of 2 or 3 young (P = 0.25).

Territories that fledged more young exhibited less diversity in the prey items captured (Fig. 3.7). There were significant differences in standardized diet breadth among sites of different productivity when the effect of the number of prey items collected was controlled for in ANCOVA (Table 3.4). There was no significant interaction between the number of prey items and brood size. Bonferroni post-hoc comparisons showed that territories with 1 young had significantly greater dietary diversity than did territories with
FIGURE 3.6. Mean prey biomass (± 1 S.E.) of Peregrine Falcons breeding along the Yukon River, Canada, relative to the number of fledged young from 2003 and 2004.
TABLE 3.2. Mean biomass of prey in relation to brood size of Peregrine Falcons breeding along the Yukon River, Canada, from 2003 and 2004, determined by a general linear model.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>$F$</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>988949.04</td>
<td>1</td>
<td>988949.04</td>
<td>694.79</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Year</td>
<td>36.69</td>
<td>1</td>
<td>36.69</td>
<td>0.03</td>
<td>0.87</td>
</tr>
<tr>
<td>Brood size</td>
<td>35303.66</td>
<td>2</td>
<td>17651.83</td>
<td>12.40</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Year * Brood size</td>
<td>202.51</td>
<td>1</td>
<td>202.51</td>
<td>0.14</td>
<td>0.71</td>
</tr>
<tr>
<td>Error</td>
<td>29890.80</td>
<td>21</td>
<td>1423.37</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1270135.94</td>
<td>25</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TABLE 3.3. Mean prey biomass per nestling in relation to brood size of Peregrine Falcons breeding along the Yukon River, Canada, during 2003 and 2004, determined by a general linear model.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>267976.32</td>
<td>1</td>
<td>267976.31</td>
<td>546.59</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Year</td>
<td>615.58</td>
<td>1</td>
<td>615.58</td>
<td>1.26</td>
<td>0.28</td>
</tr>
<tr>
<td>Brood size</td>
<td>7156.04</td>
<td>2</td>
<td>3578.02</td>
<td>7.29</td>
<td>0.004</td>
</tr>
<tr>
<td>Year * Brood size</td>
<td>818.08</td>
<td>1</td>
<td>818.08</td>
<td>1.67</td>
<td>0.21</td>
</tr>
<tr>
<td>Error</td>
<td>9805.32</td>
<td>20</td>
<td>490.27</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>332382.64</td>
<td>25</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
FIGURE 3.7. Diversity of prey (± 1 S.E.) used by Peregrine Falcons breeding along the Yukon River, Canada, relative to the number of fledged young in 2003 and 2004.
TABLE 3.4. Diet diversity of breeding Peregrine Falcons in relation to brood size (1, 2, 3 young) along the Yukon River, Canada, during 2003 and 2004, determined by a general linear model, controlling for the effect of number of prey items as a covariate.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.18</td>
<td>1</td>
<td>0.180</td>
<td>145.73</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Brood size</td>
<td>0.007</td>
<td>2</td>
<td>0.004</td>
<td>2.99</td>
<td>0.074</td>
</tr>
<tr>
<td>Number of prey</td>
<td>0.023</td>
<td>1</td>
<td>0.023</td>
<td>18.26</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Brood size * Number of prey</td>
<td>0.004</td>
<td>2</td>
<td>0.002</td>
<td>1.80</td>
<td>0.19</td>
</tr>
<tr>
<td>Error</td>
<td>0.023</td>
<td>19</td>
<td>0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>2.11</td>
<td>25</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
3 young \( (P = 0.03) \), but there were no significant differences between territories with 1 or 2 young \( (P = 0.38) \) or 2 and 3 young \( (P = 0.59) \).

Territories with more young were associated with higher counts of waterfowl on each territory \( (\text{Kruskal-Wallis } H_2 = 8.16, P = 0.04) \). Non-parametric rank comparisons \( (\text{Dunn 1964, as cited in Zar 1998}) \) showed that territories that produced at least 3 young had significantly greater waterbird abundance than less-productive territories \( (Q > 2.64 \text{ for all comparisons, } P < 0.05) \). There were no other significant differences observed in either prey or biomass classes between territories of differing productivity.

DISCUSSION

PREY USE BY BREEDING PEREGRINE FALCONS

Peregrine Falcons rarely bring prey items to the ledge during incubation \( (\text{Nelson 1977}) \) and therefore, the prey remains I collected should represent diet during the nestling period. Although it is unlikely that all prey items used by individual pairs of birds were collected, the prey remains obtained should be representative of the prey usage by breeding Peregrine Falcons. Prey remains however, can be biased towards larger, brightly coloured prey, and may under-represent smaller prey items \( (\text{Redpath et al. 2001}) \). Efforts were made to minimize this bias by attempting to collect all feather and other remains at each nesting ledge. Additionally, analysis of prey remains only occurred from nest sites where a sufficient number of prey items \( (> 12 \text{ items}) \) were identified. While I recognize, however, that there may be biases present in the examination of prey remains, there is evidence to suggest that they are a reasonable indicator of composition of prey species \( (\text{Rosenfield et al. 1995}) \).
The use of prey by breeding Peregrine Falcons most likely represents a combination of factors that influence prey susceptibility (Hunter et al. 1988). These factors include the relative abundance, profitability, habitat associations and behaviour of the prey items, as well as characteristics of the predator, such as foraging ability (Ratcliffe 1993). In this study area, prey items that were highly abundant (sparrows, and thrushes and jays), habitat generalists (Gray Jays, American Robins), used open or riverine habitats (shorebirds, waterbirds), perched near tree tops (Lesser Yellowlegs (Tringa flavipes), American Robins, Bohemian Waxwings (Bombycilla garrulus), raptors) and were relatively energetically profitable (Northern Flickers, waterfowl) were probably more vulnerable to predation by Peregrine Falcons (Hunter et al. 1988).

The diet of Peregrine Falcons in this study area was relatively static over the period of study, as the frequency that prey classes were used did not differ significantly between years (Table 3.1); however, the high frequency of woodland species in the diet of Peregrine Falcons (Table 3.1) was surprising given that previous studies in Alaska indicated that Lesser Yellowlegs and Spotted Sandpipers (Actitis macularia) were very important prey items (Hunter et al. 1988). The higher use of woodland species (American Robins and Varied Thrushes) by foraging Peregrine Falcons in this study compared to Alaska (Hunter et al. 1988) could be due to differences in species composition between this study area and Alaska, or because species composition in both areas has changed through time. Cade (1960) concluded that when woodland birds occurred in high frequency in the diet of Peregrine Falcons, it was most likely due to attempts by these prey items to fly over the river. Anecdotal evidence from this study supports this
conclusion in that a large majority of prey captures observed over the river consisted of woodland species (B. Boukall, unpubl data).

The use of prey items according to biomass differed between years in that small prey items (< 50 g) were taken significantly more frequently in 2004 (Fig. 3.1). Possible explanations for this difference in use between years revolve around forest fires that occurred in the region in 2004. These fires could have caused larger prey species (e.g., waterfowl) to emigrate out of the area to seek immediate, more favourable conditions and caused a shift in the diet of peregrines to include a greater number of smaller species. Waterfowl and other waterbirds commonly migrate from a region stricken with drought to habitat with more favourable conditions (Hestbeck 1995, Niemuth and Solberg 2003) and so it seems reasonable that they may disperse in response to fire. Reductions in prey have been indicated as a major factor affecting the reproductive output of the American Kestrel (*Falco sparverius*) breeding in an area stricken by fire (Dawson and Bortolotti 2006). Additionally, decreased visibility resulting from the fires may have reduced the ability of foraging peregrines to detect prey in the environment. This would decrease the hunting distance available for foraging peregrines, forcing them to hunt prey closer to perch sites. Smaller prey items such as warblers, swallows and some species of sparrows were observed in greater abundance along the nesting cliff face (B. Boukall, pers. obs.).

**RELATIONSHIPS BETWEEN PREY USE AND PRODUCTIVITY**

There were large differences in the productivity of the peregrine population between 2003 and 2004, with nests fledging a greater mean number of young in 2003. This may
be attributable to both forest fires and density-dependent regulation processes acting on productivity in 2004 (see Chapter 2 for details).

To raise large broods, it is necessary that parents, especially the male, be efficient foragers so that they are able to provide adequate nutrition for growing young without impinging on their future survival and lifetime reproductive output (Deerenberg et al. 1995). The amount of biomass brought to the nest increased with brood size, but the amount of prey per nestling decreased with increasing brood size (Figs. 3.6 and 3.7). These results are consistent with the conclusions of other researchers. Enderson et al. (1972) found that larger broods of Peregrine Falcons in the Alaskan interior were fed more often, but individual nestlings received fewer feedings, and less food per individual. As in this study, average prey biomass increased with brood size, and smaller broods received fewer large items (Palmer et al. 2004). Olsen et al. (1998) demonstrated that larger broods receive more parental effort and an increased amount of prey biomass during the nestling period.

Despite receiving less biomass per nestling in larger broods, nestlings were still able to grow and fledge successfully, and indeed, nestlings are able to grow and fledge successfully on widely varying amounts of prey (Newton 1979). Food requirements of nestlings are influenced by the combined effects of weather, nest characteristics, brood size, prey delivery rates and nestling activity (Boulet et al. 2001). For example, larger brood size is associated with lower thermoregulatory costs and therefore less food per individual is required to maintain homeothermy in these nests (Royama 1966). Dawson and Bortolotti (2003) hypothesized that increased food requirements of young in smaller broods may be due to increased energetic costs, especially at higher latitudes with low
temperatures during the breeding season. Parents may choose to raise larger broods when
nesting in adequately protected nest sites and during periods of higher prey abundance. 
Because larger broods have lower costs of thermoregulation, parents should be able to
raise these large broods more efficiently.

SELECTION OF PREY BY BREEDING PEREGRINE FALCONS

Breeding Peregrine Falcons were selective predators and exhibited non-random
utilization of prey, in terms of both biomass and prey classes (Figs. 3.3 and 3.5).
Peregrine Falcons breeding along the Yukon River appeared to select prey based on
relative profitability by using prey items weighing between 50 and
500 g to feed nestlings, with medium-sized prey items (251-500 g) being used greater
than their availability (Fig. 3.3). Male peregrines capture the majority of prey items
brought to the nest during the breeding season (Olsen et al. 1998) and the body mass of
male peregrines (611 g; Dunning 1993) relative to prey items can most likely explain my
results. Studies have shown that male peregrines hunt medium- and small-sized birds
more successfully than females (Thiollay 1988, Jenkins 2000), presumably due to the
male’s smaller size and greater aerial manoeuvrability (Andersson and Norberg 1981).
Larger prey items, such as waterfowl, generally do not appear in the diet of nestlings until
the female begins to forage (Rosenfield et al. 1995) after the young have reached
thermoregulatory independence (21 days; Enderson et al. 1972). Foraging Peregrine
Falcons, however, did not exhibit significant selection for any one biomass class,
implying that Peregrine Falcons can be quite flexible meeting the nutritional
requirements of nestlings.
Of the 10 prey classes identified, waterbirds were the most selected prey items, followed by shorebirds (Fig. 3.5). Waterbirds were the main contributor to biomass at the nest site (Table 3.1), and thus comprise a major nutritional component for developing young. In addition, shorebirds, woodpeckers and thrushes and jays were used in greater proportion than their abundance, although the use of both woodpeckers and thrushes and jays were not significantly greater than their abundance (mean selection coefficient not significantly greater than 0) (Fig. 3.5). The probability of predator-prey encounters between peregrines and thrushes and jays was most likely higher than other selected prey classes, because there were higher territorial abundances of this prey class (Fig. 3.4). The higher prey availability would lower the selection coefficient for this group, so that thrushes and jays were taken in accordance to their abundance. Thrushes and jays were used more frequently than any other prey class by foraging Peregrine Falcons (Table 3.1), and using a highly abundant, relatively profitable prey source (~75 g) would help meet the nutritional needs of the young and brooding female.

The selection for the woodpecker prey class was surprising given that the majority of these species tend to remain in vegetative cover (Short 1982), and thus are rarely exposed to aerial pursuits by foraging peregrines. Larger woodpecker species, such as the Northern Flicker (*Colaptes auratus*), which comprised the majority of woodpecker species taken, would be energetically profitable and the wing colour patches may attract the attention of foraging falcons (Hunter et al. 1988).

Selection coefficients are based on proportions, however, and can erroneously indicate strong selection or avoidance of rarer prey classes because smaller absolute differences in use and availability are much larger proportionately (Marzluff et al. 1997).
This problem may have resulted in some prey classes appearing to be selected whereas others were avoided, and the preferential use of medium-sized prey items (251-500 g) and Woodpeckers, both of which were not abundant on territorial prey counts (Figs. 3.2 and 3.4).

Detectability of prey during counts of abundance may result in biases in the data. Smaller or quieter species would be less frequently encountered and thus be represented as fewer individuals in the indices of prey abundance from a territory, while louder species would be more frequently encountered. Nonetheless, I do not expect large biases in my data because the majority of detections occurred within 75 m from the point at which counts occurred (> 89% of all detections for all counts). I am therefore reasonably confident that my counts are representative of prey abundance in the foraging area of nesting Peregrine Falcons.

THE EFFECT OF SELECTED PREY ABUNDANCE ON PRODUCTIVITY OF PEREGRINE FALCONS

The relative abundance of waterbirds observed at a territory was significantly related to brood size in this study. Waterbirds contributed largely to the prey biomass (Table 3.1) brought to the nest and represent the most selected prey of breeding Peregrine Falcons (Fig. 3.5). Larger prey items are generally captured and brought to the nest by females (see above). The provisioning rate of females, however, was unrelated to brood size in Australian Peregrine Falcons (Falco peregrinus macropus) and breeding success was largely due to male effort and ability (Olsen et al. 1998). The biomass brought to the nest by the female, however, may be more important than the rate of provisioning. Increased
biomass provided when young are undergoing rapid development is a major factor affecting brood success (Palmer et al. 2004). Female falcons generally tend to remain close to the nest site (Nelson 1977), and an increased abundance of energetically profitable prey types (e.g., waterbirds) proximal to the nest site would result in increased female foraging efficiency, meeting the nutritional requirements of increased brood size. Different conditions along the river valley may be more favourable as staging and nesting areas for waterfowl. If appropriate habitat conditions for waterfowl are present within a territory, higher rates of waterbird predation by Peregrine Falcons could be expected. The counts performed in this study may be an indicator of these conditions and could also relate to the quality of a territory.

Selective foragers will feed more exclusively on their selected prey type when it exists in greater abundance (Stephens and Krebs 1986), resulting in decreased diet diversity. A study of prey selection by Merlins (Falco columbarius) determined that the abundance of selected prey was negatively correlated with overall diet diversity (Sodhi and Oliphant 1993). My results are in agreement with this finding, as more productive territories (3 young) had significantly lower diet diversity. Diet diversity, however, exhibited no relationship with the abundance of selected prey (waterbirds) in the territorial environment. Possible reasons for why these results do not mirror the results from the Merlin study (Sodhi and Oliphant 1993) are that I examined the use and abundance of prey groups as opposed to individual species. The grouping of prey species into classes was done to ensure an adequate sample size for analysis. Secondly, waterbirds may represent an opportunistic, transient food resource in this study area along the Yukon River, taken whenever they become available. These larger prey types,
while highly selected, may never be consistently abundant on a territory, and therefore the diet diversity of peregrines may not be related to the abundance of waterbirds.

CONCLUSION

In summary, these results suggest that breeding Peregrine Falcons are selective predators. The use of prey by breeding Peregrine Falcons was most likely influenced by accessibility, abundance and energetic efficiency. More productive pairs brought more biomass to nests, and exhibited lower diversity in their diet, implying that selected prey was more accessible, parental foraging was selective and efficient, or possibly a combination of both. Similar to other studies on food habits of Peregrine Falcons, my results indicate that Peregrine Falcons feed on a wide range of prey species, and do not exhibit much dependence on any one item. The results do, however, suggest that the proximity of the most selected prey (waterbirds) is important for productivity. The availability of energetically profitable prey types, such as waterfowl, was associated with increased brood size. Because of sexual size dimorphism, the female probably captures and retrieves larger prey items. The relationship between prey biomass and brood size implicates the importance of female provisioning for reproductive success.

In this study, I was not able to evaluate the influence of parental quality and distinguish between parental hunting efficiency relative to territorial prey abundance. Future studies are needed to distinguish parental prey selection and parental foraging efficiency relative to age and experience. This information will be essential to test foraging theory as it relates to reproductive output.
4. GENERAL DISCUSSION

Environmental factors combine to regulate and influence the dynamics of populations. In this study, territory quality, precipitation during the nestling period, forest fire events, and prey use and abundance, all had roles in determining the productivity for this population of Peregrine Falcons (*Falco peregrinus anatum*). This is one of the few studies that has investigated an array of environmental factors that influence the reproductive output of peregrines. As such it has allowed me to provide information about how these factors may act together to regulate and limit bird populations, and specifically those of peregrines, in the wild.

INTEGRATION OF VARIABLES IN THE ENVIRONMENT AND THEIR EFFECT ON THE REPRODUCTIVE ECOLOGY OF PEREGRINE FALCONS IN THE NORTH

It is important to understand the mechanisms that influence population dynamics, especially for conservation purposes (Sutherland 1996). An important goal of conservation is to understand how these mechanisms drive fluctuations in population size, while preventing extinctions at lower densities (Wiklund 2001). The aim of this thesis was to examine how territory quality, weather conditions, and prey use interact to regulate and limit the productivity of Peregrine Falcons. Given that a multitude of factors influence the environment occupied by individuals, it is important to determine how environmental factors can interrelate to influence the breeding dynamics of populations.
THE RELATIVE IMPORTANCE OF DENSITY-DEPENDENT AND INDEPENDENT PROCESSES TO THE REPRODUCTIVE ECOLOGY OF PEREGRINE FALCONS

The productivity of Peregrine Falcons breeding in the Yukon was influenced by weather conditions, which affected population dynamics independent of density. I found that visibility also had an influence on the numbers of Peregrine Falcons breeding in the Yukon (Fig. 2.6), probably by mediating foraging conditions. This study is one of the few studies to document weather influences on the rate of occupation by Peregrine Falcons, and implicates the importance of food availability for the occupation of breeding territories.

Precipitation conditions during the nestling period had a similarly significant influence on breeding Peregrine Falcons. My results provide support for previous research that rainfall during the early nestling period is a strong determinant of productivity in Peregrine Falcons (Mearns and Newton 1988). Increased rainfall during the early nestling period when the young are unable to independently thermoregulate (Bradley et al. 1997) resulted in a decreased number of breeding pairs successfully fledging young in my population of Peregrine Falcons (Fig. 2.7a). It is probable that a combination of increased nestling energetic demands and lower food intake is responsible for the decreased productivity (Tinbergen and Dietz 1994, Siikamäki 1996, Dawson and Bortolotti 2000).

Precipitation after the period of thermoregulatory independence (young > 21 days old) significantly influenced the mean number of fledged young each year (Fig. 2.7b). Precipitation most likely mediated the availability of prey, possibly resulting in starvation.
of the young. Weather conditions act as the ultimate factor influencing productivity of Peregrine Falcons in this study, because weather conditions appear to affect aspects of foraging and thermodynamics of young. The influence that territorial quality has on productivity also can be mitigated by weather conditions, as favourable weather conditions may allow individuals nesting in poorer territories to produce offspring. Given the relatively short breeding seasons in the north, alterations of weather conditions as a result of changing climate could also have far-reaching consequences for foraging behaviour and subsequent productivity of breeding birds in the north.

Nest placement and characteristics of the nest site affected the reproductive output of Peregrine Falcons by influencing the nest microclimate and the level of protection offered to the young from environmental conditions. Nesting ledges that offered more protection from environmental factors produced more offspring than sites lacking these characteristics. Specifically, the presence of an overhang, adequate ledge depth, decreased accessibility by predators, and narrower river channel widths (Fig. 2.1) were important aspects of breeding habitat for Peregrine Falcons in the Yukon. Protection from the environment would conceivably reduce the energetic requirements of the young, thereby reducing the probability of starvation during periods of poor weather. Decreased river channel width may have facilitated prey capture by increasing hunting efficiency (see below).

DENSITY-DEPENDENT LIMITATION THROUGH SITE-DEPENDENT REGULATION
One of the key features necessary to test the site-dependent regulation hypothesis (Rodenhouse et al. 1997) is the identification and measurement of habitat quality (Sergio and Newton 2003). Theoretically, territories that offer a greater abundance of resources, resulting in increased survivorship and fecundity, should be used more frequently than other territories (Pulliam and Danielson 1991). In this study, peregrines breeding in frequently occupied territories produced on average a greater number of young (Fig. 2.2). The results of this study, therefore, provide additional support for the use of territorial occupancy as a measure of habitat quality (Sergio and Newton 2003). Frequently occupied territories were located on narrower sections of the river and along longer cliff sections. These attributes of the territory could conceivably be associated with increased foraging efficiency (Jenkins 2000) and may therefore link food availability with nest occupancy. This may also partially explain why more birds fledged from higher quality territories during the forest fire in 2004.

According to the site-dependent regulation hypothesis, the use of progressively less-suitable sites by a growing population should reduce the average productivity for the population as a whole (Rodenhouse et al. 1997). Crowding and territoriality mechanisms as represented by nearest known neighbour distance did not have a significant influence on the number of fledged young from a site. The average quality of occupied territories decreased with increasing density in this population (Fig. 2.4), followed by a subsequent decrease in annual reproductive output, providing evidence for site-dependent regulation. This population, however, only partially conformed to the theory of site-dependent regulation, and reproduction was also influenced by other factors in the environment, namely precipitation during the nestling period and the forest fire that occurred in 2004.
This study was able to demonstrate the importance that stochastic events, such as the forest fire that occurred in 2004, can have on the productivity of a population. The forest fire of 2004 appeared to amplify the effect of territorial quality as more young were produced at sites of higher quality, which may also be related to foraging efficiency.

The effect that ledge-site characteristics, weather conditions and territorial quality had on the productivity of Peregrine Falcons implies that mechanisms operating at both the larger regional scale and the scale of the nest site influence the dynamics of populations. While the data collected were not conducive for modelling the variables at different scales, I assume that these factors operate simultaneously to influence population productivity. Territorial quality, however, was the only significant factor in the model explaining variation in the mean annual number of young fledged when all years were considered. Higher territorial quality in this study was associated with higher rates of occupation and reproductive output. Factors including the quality and age of the parents most likely have a large role in determining the reproductive success and future occupation of a territory. The availability of prey appears to also play a large role in determining the reproductive output of Peregrine Falcons (Boutin 1990), and thus the quality of a territory. It is therefore probable that higher quality territories produce greater number of young because they are also associated with higher abundances of prey.

PREY USE, ABUNDANCE AND SELECTION BY BREEDING PEREGRINE FALCONS

Food availability often determines the reproductive output of organisms, and thus variable food supplies can act to limit productivity (Hogstedt 1981, Martin 1987). This
study examined the relationships between productivity and the use, abundance and selection of prey by individual pairs of peregrines. My results provided evidence that peregrines are selective predators. The use of prey was most likely influenced by a combination of prey accessibility, prey abundance and the energetic efficiency of prey.

The diet of Peregrine Falcons was relatively static over the period of study (Table 3.1), although smaller prey items (< 50 g) were more prevalent in the diet of Peregrine Falcons in 2004. Forest fires may have decreased the availability of larger prey items, through either reduced visibility or emigration of such prey. Similar to other studies on food habits of Peregrine Falcons (Cade 1960, Sherrod 1978, Hunter et al 1988, Rosenfield et al. 1995), my results indicate that Peregrine Falcons feed on a wide range of prey, and do not exhibit much dependence on any one item. My results do, however, demonstrate the influence of proximity of highly selected prey (waterbirds) on productivity. The availability of energetically profitable prey types, such as waterfowl, was associated with increased brood size. As a result of sexual size dimorphism, the female captures and retrieves larger prey items, and so the relationship between prey biomass and brood size implicates the importance of female provisioning.

To raise large broods, parents must be effective foragers to provide adequate nutrition for young, without impinging on their own future survival and fecundity (Ricklefs 1968, Trivers 1974, Stearns 1992, Martin 1995). Breeding pairs with larger broods brought a greater overall mean prey biomass to nests (Fig. 3.6), but mean prey biomass per nestling decreased in larger broods. More productive pairs exhibited lower diversity in their diet, implying that selected prey was more accessible, parental foraging was selective and efficient, or possibly a combination of both. Brood size may reflect the
foraging efficiency of the parents (Palmer et al. 2004), and as such highly efficient
foragers may raise larger broods. Additionally, parents may be able to raise larger broods
when nesting in adequately protected nest sites and during periods of higher prey
abundance, and because larger broods have relatively lower costs of thermoregulation,
parents are also able to raise these large broods more efficiently.

RESPONSE OF PEREGRINE FALCONS TO CHANGING ENVIRONMENTAL
CONDITIONS: FUTURE RESEARCH DIRECTIONS
The preferential use of habitat and prey may result in differences in productivity among
pairs, therefore having evolutionary consequences. The fact that a high proportion of
young are produced from a small number of high-quality territories raises the possibility
of phenotypic selection for individuals that choose higher quality habitat (Sergio et al.
2003), presuming that offspring recruit locally to similar territory types when available.
Although post-fledging survival of young was not measured in this study, there is a high
probability that the majority of individuals in the next generation are produced from
higher quality territories (Sergio and Newton 2003). Studies focusing on genetically
distinguishing individuals on the basis of their nest choice behaviour and subsequent
fecundity would provide support for the adaptive, phenotypic selection of nesting habitat
(Sergio et al. 2003). The behaviour and experience of individuals can either act in concert
or antagonistic to the site-dependent hypothesis. The knowledge of how individuals select
both nest sites and breeding territories, coupled with the genetic makeup of individuals in
the population, would further our understanding of how site-dependent regulation
mechanisms operate with respect to natural selection.
Precipitation had a large effect on the reproductive output of Peregrine Falcons and is extremely important in northern populations, where the climate appears to be rapidly changing (Hebda 1997). Alteration in precipitation conditions, especially during the month of July when young have large energetic requirements, coupled with reductions in territorial quality, could have important implications for the population dynamics of Peregrine Falcons. Future research should examine the consistency of territorial quality relative to changing environmental conditions (e.g., effects of forest fires on long-term territorial quality). Additionally, to further our understanding of how mechanisms of regulation influence population dynamics, future research should separate the influence of habitat quality from individual quality in determining the production of young.

The higher use of woodland species by peregrines in this study and the relatively high rate of reproductive output compared to observations in Alaska (Hunter et al. 1988) indicate that Peregrine Falcons are very plastic in meeting their nutritional requirements. Foraging plasticity may be an important characteristic determining successful breeding. The difference in prey use and selection by different breeding pairs may be related to territory selection, and if so reinforces phenotypic selection. Natural selection should favour those pairs that occupy higher quality sites and forage on highly selected prey types to consistently produce greater numbers of young. The forest fire in 2004 appeared to have some effect on prey use by Peregrine Falcons. Given that avian communities experience large changes after fire (Saab and Powell 2005), future studies should examine differences in habitat quality and food availability between burned and unburned sites, and the relation to reproductive success of Peregrine Falcons.
LOOMING HORIZONS: MANAGEMENT IMPLICATIONS AND CONSERVATION OUTLOOK

The dynamics of populations are influenced by multiple environmental factors at multiple scales. An understanding of how these factors interrelate is crucial for the conservation of populations in rapidly changing environments. Populations of Peregrine Falcons in the Yukon have experienced dramatic variation in their reproductive output between 2000 and 2004 (D. Mossop and B. Boukall, unpubl data). This study has shown that the combination of habitat quality, precipitation during the nestling period, forest fire events, and prey use and abundance, all play important roles in governing population productivity and subsequently population dynamics. Given the number of high-quality sites available and the peregrine’s ability to selectively forage, it would appear that there is a positive outlook for Peregrine Falcon populations in the Yukon. The recent delisting of the Peregrine Falcon from the Endangered and Threatened Species list, as well as recent surveys from across North America supports this claim (Cade et al. 1997, Rowell and Stepinisky 1997, Millsap et al. 1998, Holroyd and Banasch 2000). Accumulation of pollutants in the north (Muir et al. 1997, Norstrom et al. 1998, MacDonald 2005), as well as possible consequences of climate change, however, suggest that wildlife managers should be conservative when ascertaining population health. The use of territorial quality in the site-dependent regulation model allows wildlife biologists to better understand the trends and dynamics of many bird populations, including Peregrine Falcons. Dramatic decreases in production at higher quality sites may be signalling negative changes in the environment. Wildlife professionals should use this information to better understand the
population dynamics of raptor species and to better manage these populations in the
north.
LITERATURE CITED


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APPENDIX I: CHARACTERISTICS OF NEST-SITES USED BY PEREGRINE FALCONS BREEDING ALONG THE YUKON RIVER, CANADA, IN 2003.

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* Frequency in which nests were occupied out of 11 years

Easily accessed sites were ranked 1, while sites with near impossible entry were ranked 5.

* 0 = no overhang, 1 = overhang present
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<th>Qualityb</th>
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*a Frequency in which nests were occupied out of 11 years

*b Ranking quality of nests based on occupation frequency, 1 = 0.67 - 1.00, 2 = 0.33 - 0.67, 3 = 0.00 - 0.33

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